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K. P. OAKLEY

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SOME PEARL-BEARING CERAMOPORIDAE (POLYZOA)

BY

KENNETH PAGE OAKLEY, D.Sc.

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SOME PEARL-BEARING CERAMOPORIDAE (POLYZOA)

By KENNETH P. OAKLEY

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SYNOPSIS

Studies of British and Swedish ceramoporid Polyzoa resulted in an emendation of the generic diagnosis of *Favositella*, in the recognition of two new species of this genus and of several 'formae' of the type species. The known pearl-bearing Polyzoa are referred to four species: *F. interpuncta* (Quenstedt), *F. squamata* (Lonsdale), *F. anolotichoides* sp. nov., and *F. gotlandica* sp. nov. The first three species are found in the Wenlock and Ludlow Series of Britain, the fourth in the Gotlandian formation of Sweden. In Britain the pearl-bearing *Favositella* stock ranges from the Woolhope Limestone to the Aymestry Limestone. An account is given of various morphological characters of the Ceramoporidae as exemplified by *Favositella*. It is suggested that the extra-macular zooecia were occupied by autozooids, and the mesopores by nanozooids. Evidence is adduced that maculae were the seat of reproductive processes, and it is suggested that they were sometimes converted into brood-chambers, the large macular zooecia having lodged gonozooids. The wide range of morphological facies exhibited by some species of *Favositella*, notably *F. interpuncta* (Quenstedt), is attributed to the varying effects of different environmental factors on the development of the zoarium. To express differences of this order a number of formae are established.

I. INTRODUCTION

PRELIMINARY studies of the Polyzoa of the Wenlock Limestone showed that a number of Ceramoporidae contained pearl-like phosphatic calculi which had been formed during life, sometimes around "brown bodies", and occasionally embalming the secondary embryo of a polypide (Pl. 1, fig. 1). That these phosphatic "pearls" were formed most commonly in species of the genus *Favositella* at a time when this genus was approaching extinction suggested that they represented a physiological defect to which members of this stock were prone. The structure, mineralogy, and mode of occurrence of calculi in *Favositella* have already been described in detail, and the probable biochemical factors involved in the deposition of phosphate in coelomic fluid analysed as far as possible (Oakley 1934). There remained the need to publish a systematic account of the species of *Favositella* found to contain calculi.

Professor N. Spjeldnaes (Copenhagen) informed the author (personal communication, 1951) that he had found similar but smaller phosphatic calculi in old (gerontic?) individuals of a few non-ceramoporoid Polyzoa (e.g. in an Ordovician species of the trepostome *Dianulites*, and in a Gotlandian species of the cryptostome *Ptilodictya*). He confirmed the author's observations regarding optical properties and chemical composition of polyzoan calculi and fully agreed that the deposition of phosphatic matter was probably a sign of degeneration. Professor Spjeldnaes added the interesting observation that to a vertebrate palaeontologist the phosphatic calculi of Polyzoa are practically like globular calcified cartilage.

II. SYSTEMATIC POSITION AND MORPHOLOGY OF *FAVOSITELLA*

Order CYCLOSTOMATA Busk

Suborder CERAMOPOROIDEA Bassler

Family **CERAMOPORIDAE** Ulrich

Genus ***FAVOSITELLA*** Etheridge & Foord 1884: 472

1893 *Bythotrypa* Ulrich : 324.

Type Species (by monotypy) *Favosites interpunctus* Quenstedt 1878.

The genus *Favositella* was established by Etheridge & Foord on the basis of a determination of the internal characters of *Favosites interpunctus* Quenstedt from the Wenlock Limestone of Dudley. Owing to the supposed relationships of this genus with *Favosites* it was for long regarded as a tabulate coral, but Bassler's re-investigation of topotype material (1911 : 100) showed that the type species was actually a polyzoan belonging to the generic group for which Ulrich had proposed the name *Bythotrypa*, a genus erected to include ceramoporoids with loosely constructed interzooecial tissue formed by irregular mesopores. Bassler showed that it was possible to apply Ulrich's definition of *Bythotrypa* to the type species of *Favositella* without modification. It is as follows :

> " Zoaria massive or lamellate. Zooecia forming long continuous tubes, intersected by thin diaphragms, their walls minutely crenulate and with the structure characterizing the ceramoporoids. Lunarium well defined, large, projecting above the rest of the aperture margin. Mesopores numerous, open at the surface, interiorly forming a species of vesicular tissue unusually loose and irregular in construction."

Progress in the study of ceramoporoid Polyzoa has necessitated from time to time a widening of the bases of distinction of the various genera, and *Favositella* has proved no exception to this trend. In the course of the present work further species of *Favositella* have been brought to light, and a study of these based on a large amount of material has indicated the necessity of minor modifications of the generic diagnosis. Thus the zoarium may be free or encrusting. In thin, laminate forms the mesopores are so short that there is no more than a tendency for them to form the loose vesicular tissue which characterises the genus. Relatively large, irregular pores in the zooecial walls, although not invariably present, are sufficiently common to serve as a useful guide in recognizing species. The lunarium in one newly-described species contains acanthopore-like granules.

EMENDED DIAGNOSIS. Zoaria massive or lamellate, encrusting or free. Zooecia forming tubes of variable length, usually long, intersected by thin diaphragms, their walls minutely crenulate and structure characteristic of ceramoporoids. Large mural pores commonly present. Lunarium well-defined, usually large and projecting above rest of apertural margin. Mesopores numerous, open at the surface, interiorly tending to production of species of vesicular tissue unusually loose and irregular in construction.

The characters of the family are well exhibited by *Favositella*. Externally the main distinguishing feature of the Ceramoporidae is the elevation of the frontal margin of the zooecial aperture into a hood-like structure known as the lunarium. When typically developed this accentuates any obliquity which the zooecial apertures may have, and gives an imbricate appearance to the celluliferous surface. The lunarium is usually crescentic in cross-section. Its position on the frontal side of the zooecium—the side on which the aperture of the zooid is situated in the living polyzoan—suggests that it may have had a protective function. It is formed of auxiliary ectocyst and originates as a lining of the frontal notch of the zooecium, which corresponds with the sinuation characteristic of the aperture of many Cheilostomes. While a reinforcement of the frontal margin of the zooecial aperture is not an uncommon feature in Polyzoa, the elevation of the thickened portion as a hood-like structure is a feature mainly characteristic of certain Palaeozoic groups. The lunarium is found with modifications in both families of the Ceramoporoidea (Ceramoporidae, Fistuliporidae) and also in one family of Cryptostomata (Cystodictyonidae). There is one Jurassic cyclostomatome, *Chilopora guernoni* Haime, in which the zooecia have raised zooecial lips indistinguishable from the lunaria of Palaeozoic ceramporoids (Haime 1854, pl. 10, fig. 5*b*).

The ectocyst in the Ceramoporoidea has a very distinctive character. In highly magnified thin-sections it exhibits a finely laminated structure and, at the same time, a clouded or minutely granulated appearance. It is thus easily distinguishable from the uniformly hyaline primary ectocyst of the Trepostomata. Whereas in the latter the ectocyst appears to consist of crystalline calcite, in the Ceramoporoidea (and probably in all Cyclostomata) it is not only minutely porous, but apparently composed of intimately connected, sub-microscopic fibres, perhaps originally embedded in a corneous ground-mass.

The fracture of a ceramoporoid zoarium is very different from that of a trepostome. On breaking a trepostome the walls of adjacent zooecia part cleanly down the middle; the fracture has thus a clean-cut appearance. On the other hand, when a ceramoporoid polyzoan, or for that matter any fossil cyclostome, is broken open, the fracture passes through and across walls without discrimination, and the broken surface appears dull and amorphous. The two styles of fracture are a reflexion of the histological differences between the two groups. In trepostomes the ectocyst is crystalline. Furthermore, the zooecial walls are duplex in origin so that a median plane of weakness exists between the ectocyst of contiguous zooecia. The amorphous style of fracture in ceramoporoids is an outcome of the intimately connected, perhaps felted, structure of the zooecial walls and the resulting absence of a median plane of weakness.

In *Favositella* the primary ectocyst is sometimes invested by auxiliary ectocyst. The secondary ectocyst lining the frontal end of the zooecial aperture, and constituting the lunarium, is distinguished from the rest of the zooecial wall by its lighter colour.

In common with those of most Ceramoporoidea the zoaria of *Favositella* exhibit an internal polymorphism. That is to say two types of ' cell ' are present : zooecia, and interstitial ' cells ', or mesopores. On the analogy of Recent Cyclostomata it may be assumed that the majority of the zooecia were occupied by normal polyzoan individuals, or antozooids (Borg 1926 : 188), and the mesopores by modified individuals, or heterozooids (i.e. nanozooids or kenozooids). An observation made in the course of the present work on *Favositella* tends to suggest that the mesopores were occupied by nanozooids rather than by kenozooids ; that is by zooids in which there was a simplified, but nevertheless functional, polypide. I refer to the occasional presence of dahllite calculi within the mesopores of *Favositella*. Since these pearls are believed to be the indirect result of polypide-degeneration, they are unlikely to have originated in closed ' cells ' occupied only by kenozooids (the extreme modification of zooid in which all functional organs have disappeared).

A striking feature of Ceramoporoidea (but one which they share with other Palaeozoic Polyzoa, notably the Trepostomata) is the grouping of the zooecia about regularly spaced centres composed of modified ' cells '. These centres are termed maculae. They consist of concentrations of mesopores, usually interspersed with, or surrounded by, zooecia larger than the average and thus falling into the category of topomorphs (Lang 1906 : 66). The maculae may be level with the general surface of the zoarium, but they are more commonly either slightly depressed or slightly raised (in which case they are known as monticules).

It would seem that the maculae were, in the first place, centres of growth. Thus the simple discoidal zoaria of *Ceramopora imbricata* Hall are made up of a central macula from which the zooecia radiate towards the growing edge (Bassler 1906 : 19). Similarly in more complex zoaria the frontal, or lunariate, ends of all zooecial apertures proximate to a macula. It is probable that in a mature zoarium the mesopore and enlarged zooecia in the maculae took on functions connected with reproductive processes. Ulrich has already suggested (1890 : 298) that the larger zooecia in or surrounding maculae served as the receptacles in which embryos were developed into the larval stage. He compares them with the genoecia of the Recent genus *Crisia*, which are merely slightly modified zooecia set aside for reproductive functions. Zooids adapted and transformed for the production of embryos have been termed gonozooids by Borg (1926 : 188). The heterozooids which are believed to have occupied the mesopores may have served a protective function.

In the course of investigating the Silurian species of *Favositella* a number of observations have been made which support the idea that the maculae were, at any rate at a certain stage in astogeny, the seat of reproductive processes. It has been noted that openings in the walls of zooecia and mesopores are most frequent in the maculae, while in a few mature zoaria of *Favositella interpuncta* the maculae are found to have been converted into moderately deep, stellate, or circular pits, open at the surface. These were first described by Quenstedt (1878 : 10, pl. 143, fig. 9*y* ; '*Sterngruben*') who seems to have regarded them as either pathological or due to damage during the life of the organism. It appears, however, that they have originated through the coalescence of the mesopores and zooecia in the maculae by the breaking-down, or resorption, of their walls. These pits (Pl. 3, fig. 6 ; Pl. 9, fig. 6) are so strikingly similar to the 'brood-chambers' observed in certain Recent Heteroporidae (Borg 1933 : 267, pl. 2, figs. 1, 4) that they may have served the same function. It is not improbable, on the analogy of Recent forms, that in the breeding season the walls of the mesopores and large zooecia in the maculae were partially resorbed, and that the developing embryos were discharged into the central space so formed, there to undergo larval development. However, further work on this aspect of the Ceramoporidae is required before this interpretation can be credited with any degree of certainty.

III. DESCRIPTION OF PEARL-BEARING SPECIES

Favositella interpuncta (Quenstedt)

(Pl. 1, figs. 1–6 ; Pl. 2, figs. 1–3, 6, 7 ; Pl. 3, figs. 4–6 ; Pl. 4, figs. 1–6 ; Pl. 6, figs. 1–5 ; Pl. 7, figs. 1, 2 ; Pl. 8, figs. 1, 3, 4 ; Pl. 9, figs. 6, 7)

1851 *Chaetetes Bowerbanki* (partim) Edwards & Haime : 272.
1855 *Monticulipora? Bowerbanki* (partim) Edwards & Haime : 268, pl. 63, figs. 1*b*, *c* (non fig. 1*a*).
1873 *Monticulipora* sp. 5 (partim) Salter : 109.
1873 *Monticulipora* sp. 6 (partim) Salter : 109.
1878 *Favosites interpunctus* Quenstedt : 10, pl. 143, fig. 9.
1879 *Favosites fibrosus* Sollas : 510 (vide pl. 24, figs. 12, 17–20).
1884 *Favositella interpuncta* (Quenstedt) Etheridge & Foord : 473, pl. 16, figs. 1, 1*a–f*.
1911 *Favositella interpuncta* (Quenstedt) ; Bassler : 101, text-fig. 35.

The specimen figured by Edwards & Haime (1855) as an immature form of their *Chaetetes* (*Monticulipora?*) *bowerbanki* has been found on examination to be identical with the polyzoan described below as *Favositella interpuncta* forma *texturata*. As this specimen (now preserved in the Sedgwick Museum, Cambridge : A4024) is one of the syntypes of *Chaetetes* (*Monticulipora?*) *bowerbanki*, that name must be included in the synonymy of *Favositella interpuncta*. However, it is clear that Edwards & Haime mainly based their diagnosis of *C. bowerbanki* on specimens such as the other syntype figured by them (1855 : pl. 63, fig. 1*a*). Since this specimen is a coral referable to the genus *Favosites*, it is convenient to restrict the name *bowerbanki* to forms agreeing with the anthozoan syntype, and to reject it as a name for the polyzoan on the grounds of its being a homonym.

Lectotype (here chosen). Specimen from the Wenlock Limestone of Dudley figured by Quenstedt (1878 : pl. 143, fig. 9). Preserved in the Museum of the Institute of Geology and Palaeontology at Tübingen, Germany. This is almost certainly the type since it is the only specimen preserved in the Quenstedt Collection.

Description (Pl. 2, figs. 1, 6 ; Pl. 8, figs. 1, 4). Free, roughly campanulate zoarium with spreading margins. Total height 31 mm. ; maximum diameter 47 mm. Actual thickness averages 7 mm., but locally this is exceeded owing to the superposition of two or more layers of zooecia. The deeply concave inferior surface is covered by a thin, coarsely wrinkled epitheca or epizoarial membrane ; where this is worn the nearly prostrate bases of the zooecia tend to show through (Pl. 2, fig. 6). The celluliferous surface is moderately smooth. Over the greater part of the surface the zooecial tubes have relatively thick walls and in outline are mainly rounded polygons (Pl. 8, fig. 1). There are 4 to 5 of these zooecial openings in an interval of 2 mm. The lunaria are represented by inconspicuous slightly raised thickenings of the frontal angle. In one area of the zoarial surface (Pl. 8, fig. 4) the zooecia are thin-walled and more quadrangular in outline, while the lunaria are thin, hood-like structures occupying the frontal fourth of the zooecial margin.

Open mesopores are moderately frequent ; the majority are small and circular, and occur mainly at the angles of junction of the zooecia. They are more abundant in some areas than in others.

Maculae are well developed and arranged roughly quincuncially ; the average distance separating their centres is 5 mm. They show no tendency to become monticules. Two types, or phases, can be recognized amongst the maculae. The first type, which occurs in areas where the zooecial walls are thick and the lunaria inconspicuous, is characterized by an abundance of small circular mesopores scattered amongst zooecia which are slightly larger than average. There is a tendency for the walls of the zooecia and mesopores to break down in the centre of such maculae, resulting in the formation of the stellate pits noted by Quenstedt, and now regarded as brood-chambers (p. 7). The second type of macula is associated with the other surface phase, characterized by thin-walled zooecia and conspicuously developed hood-like lunaria. Such maculae consist of a ring of large zooecia, with overarching, lunarial hoods, enclosing an irregularly-shaped area occupied by a cluster of large, thin-walled mesopores which seem to form a species of open vesicular tissue. The exposed surfaces of the adjacent lunarial hoods are marked by a series of fine lines which converge upwards and appear to be continuations of the walls of the mesopores on which the lunaria impinge.

Internal characters may be deduced from topotypes (see p. 10).

Variation in external characters. Examination of a large number of specimens of *F. interpuncta* has shown that the external variation in this species is very great, and it is found convenient to recognize a number of formae (see p. 13).

Forma *typica* (Pl. 1, figs. 4–6 ; Pl. 2, figs. 2, 3 ; Pl. 3, fig. 6 ; Pl. 4, figs. 1, 5 ; Pl. 6, figs. 3–5, Pl. 9, fig. 6). Zoaria tumular, with well-defined circular or elongate-oval outlines. Commonly such zoaria commenced their growth on some bulbous foreign body, such as a large gastropod shell, but eventually extended beyond it, so that when fully developed their margins were free epithecated expansions (Pl. 1, fig. 4). As observed by Etheridge & Foord, the form of the shell or other foreign body to which this species became attached frequently determined the external form assumed by the zoarium. This is illustrated by a specimen in the Holcroft Collection at Birmingham University (Pl. 1, figs. 4, 5). This polyzoan commenced growth on the side of a large *Loxonema*, with the result that the zoarium is broader and higher at one end than at the other and has the general form of a drumlin. Some campanulate, or tumular zoaria appear to have commenced growth on a knot of hardened mud on the sea-floor. In such specimens the base is deeply concave.

While the total height of these tumular zoaria may be as much as 50 mm., the zoarial thickness rarely exceeds 7 mm., either on account of the space occupied by the 'host' or by reason of their actual concavity (see Pl. 2, fig. 2). Where the zoarial thickness exceeds about 7 mm. there has usually been reduplication of the zooecial layers.

In forma *typica*, zoaria range in size from small bun-shaped colonies measuring 30 mm. in diameter and 12 mm. in height (e.g. B.M. N.H., D.33918) to large tumular masses 90 mm. in length, 60 mm. in width and 30 mm., or more, in height.

The zooecial apertures are relatively thick-walled and present the form of rounded polygons. Lunaria are inconspicuous, usually little more than blunt processes. Thin-walled quadrangular zooecia, with prominent cowl-like lunaria, are only present when there has been new growth. This type of surface is regarded as constituting a distinct forma (see last paragraph below).

Mesopores are small and scattered, and have the appearance of pin-pricks in the thickened angles of junction of the zooecial walls. Typically the maculae are inconspicuous (cf. first type in lectotype), but in some zoaria they are raised into low monticules (Pl. 1, fig. 6). Occasionally the zooecia and mesopores in the maculae have become confluent through break-down of the walls, thus giving rise to conspicuous pits which in all probability served as brood-chambers (see p. 7 and Pl. 3, fig. 6; Pl. 9, fig. 6).

Forma *brevipora* (Pl. 2, fig. 7; Pl. 4, figs. 2, 6; Pl. 6, figs. 1, 2; Pl. 9, fig. 7). This forma is typically exhibited by thin zoaria encrusting the surface of smooth-shelled brachiopods such as *Meristina tumida* (Dalman), and more rarely tumid gastropods such as *Poleumita globosa* (Schlotheim). The thickness of the zoarium is normally 2–3 mm.; the surface is remarkably smooth and maculae are inconspicuous. The zooecial walls are thickened distally with the result that the apertures are sub-polygonal or rounded. Small circular mesopores, occurring at the zooecial angles, are relatively abundant, particularly in the maculae. A local tendency to linear arrangement of the zooecia is occasionally noticeable.

Forma *texturata* (Pl. 3, fig. 5; Pl. 4, fig. 4; Pl. 7, fig. 2; Pl. 8, fig. 3). This facies is also typically expressed when the whole zoarium is a thin encrusting sheet, as on smooth-shelled brachiopods such as *Meristina tumida* (Dalman), or *Gypidula galeata* (Dalman). Over the whole surface the zooecial apertures are arranged in a regular lace-like pattern, a dominant feature of which is the occurrence of sharply defined star-like maculae in quincunx. Each macula consists of an irregular ring of five or six large zooecia with prominent, usually finely ribbed, lunarial hoods which face away from a slightly depressed area of thin-walled, angular mesopores. The bases of the lunarial hoods of the large zooecia occupy about a third of the whole circumference of the zooecial aperture.

The zooecia outside the maculae are thin-walled and mainly quadrangular. They are slightly larger than in the forma *typica*, there being $3\frac{1}{2}$ to 4 in an interval of 2 mm. They have small but prominent lunaria, the frontal or external surface of which is rounded and sometimes marked by fine ribs converging upwards. Mesopores are almost entirely confined to the maculae.

All zooecia are oriented with respect to some macula. The intersection of the zones of propagation of the several maculae has resulted in the surface being divided up into variously shaped sectors, within each of which the lunarial hoods have the same direction, and across the boundaries of which the orientation of the zooecia changes. Within each sector of constant orientation the zooecia consequently have a very characteristic appearance (rather like that of a net pulled from various centres) which is markedly different from that of the forma *typica*. Nevertheless, the fact that areas of new growth in typical zoaria closely approximate to the *texturata* condition (see p. 13, and Pl. 8, fig. 4), is proof that this form is largely transitory.

Forma *irregularis* (Pl. 4, fig. 3 ; Pl. 7, fig. 1). Zoaria forming irregular crusts on the surface of gastropods, corals and brachiopods. The zoarium usually has a very uneven surface, and varies in thickness from 2 mm. to 10 mm. The character of the surface shows an irregular transition from that of forma *typica* to that of forma *texturata*. The two types of surface-character are so intimately mixed that the zoaria have a distinctive appearance. Maculae are unevenly distributed, and very variable in structure, although the type associated with the pure *texturata* condition predominates. There are on the average 4 zooecial apertures in 2 mm.

Forma *intermedia* (Pl. 3, fig. 4) only differs from *irregularis* in mode of origin of the zooecial irregularity (see p. 14).

Description of internal characters. These have been studied in topotype material.

Forma *typica* (Pl. 4, figs. 1, 5 ; Pl. 6, figs. 3–5). In tangential sections (Pl. 4, figs. 1, 5) the majority of the zooecia appear as irregularly rounded polygons with an average diameter of 0·4 mm. Such zooecia have an indistinct lunarium occupying a notch in the frontal margin. The zooecial walls in the mature zone of a typical zoarium are relatively thick (*circa* 0·05 mm.), and are formed of coarsely lamellar, crypto-fibrous tissue. The lunaria are formed of more pellucid tissue. Sporadic breaks can be observed in the zooecial walls and indicate the occurrence of large mural pores. Mesopores appear as rounded or oval spaces 0·1 mm. to 0·2 mm. in diameter, and occur at the angles of junction of the zooecial walls. They are noticeably more abundant in the maculae.

The occurrence of areas in which the zooecia show linear arrangement, sub-ovate, quadrangular, or subtriangular outlines, and more distinct, pointed lunaria, indicates that the section has passed into an immature zone in which there is an approach to the *texturata* condition.

In deeper transverse sections through the mature region the zooecia and mesopores have thinner walls and appear more angular in outline ; irregularly pentagonal and sub-triangular outlines predominate amongst the zooecia. In macular areas the zooecia show elongate outlines with a longer axis measuring as much as 0·6 mm. Breaks in the walls are relatively common and lead occasionally to meandrine zooecial spaces. The lunaria are inconspicuous, each being represented by a small triangular patch of light-coloured tissue in the frontal angle of the zooecium.

Transverse sections through the sub-ephebic levels show rather quadrangular zooecia arranged in diagonal rows, recalling the *texturata* condition fully described below.

Vertical sections through typical zoaria (Pl. 1, fig. 3 ; Pl. 6, figs. 3–5) show one to three layers of zooecia varying in thickness from 3 mm. to 12 mm. Each layer has a thin basal lamina. In free expansions the basal lamina of the lowest zooecial layer is coated by a thin, corrugated epithecal membrane. The zooecial tubes arise obliquely from the basal lamina (Pl. 6, fig. 3), but after a short distance become more or less vertical. In the mature zone mesopores are locally intercalated between the zooecia.

The walls of the zooecia are irregularly crenulate ; in sufficiently thin sections it is possible to detect small, and often rather oblique, mural pores. When a vertical section cuts a zooecial wall tangentially the ectocyst is seen to have a transversely laminated structure. The zooecial walls sometimes show oblique, upwardly directed, spine-like processes jutting into the zooecial cavity (Pl. 6, fig. 3). It is unlikely that these are comparable with the spines observed in certain trepostomes (Cumings & Galloway 1915 : 358) ; they more probably represent incipient mesopores. Thin diaphragms occur at intervals throughout the zooecial tubes ; they are slightly convexo-concave in the upward sense, and are separated by an interval generally varying from one to two tube-diameters.

Mesopores tend to be loosely vesicular in character. Their walls contract and expand in an irregular manner so as to produce a roughly moniliform effect (Pl. 1, fig. 3 ; Pl. 6, fig. 5). In some cases the mesopores are cut up into vesicles by oblique or transverse projections of the wall, similar to those already noted in the zooecia. Thin diaphragms occur sporadically in the mesopores. The walls of the mesopores in fully mature zoaria are thickened near the surface.

Forma *brevipora* (Pl. 4, figs. 2, 6 ; Pl. 6, figs. 1, 2). Tangential sections of zoaria in this condition do not differ materially from those of forma *typica*. Mesopores are variable in size and frequency. The zooecia present mainly sub-polygonal, rounded or oval outlines with an average diameter of 0·4 mm. ; lunaria are indistinct.

Vertical sections show that the zooecia become erect after an abbreviated oblique phase. The essential differences from forma *typica* are : (i) the shortness of the mature zone ; and (ii) the simplicity of the mesopores, which are formed by a bifurcation of the zooecial wall, as in forma *texturata*.

Forma *texturata* (Pl. 4, fig. 4 ; Pl. 7, fig. 2). Tangential sections bring out the marked linear arrangement of the zooecia within circumscribed sectors. The zooecia are predominantly quadrangular in outline, although some may show oval or rounded pentagonal cross-sections. They are thinner walled (average thickness, 0·035 mm.) than in forma *typica*, and vary in diameter from 0·4 mm. to 0·5 mm. The lunaria of all zooecia are sharply defined, and usually sagittate in outline (Pl. 4, fig. 4). Small rounded mesopores occur, but are almost entirely confined to the maculae.

Vertical sections (Pl. 7, fig. 2) are indistinguishable from those through the proximal region of forma *typica*. They bring out the shortness and obliquity of the zooecia typical of this form. Lunaria are difficult to distinguish in vertical sections, but are clearly direct prolongations of the frontal walls of the zooecia, lined internally with auxiliary ectocyst. Mesopores are shallow and thin-walled. Each is formed by the bifurcation of a ' septum ' from the upward-facing, or basal surface of a zooecial wall, usually at a distance of 0·5 mm. to 1·0 mm. above the basal lamina. There is no epitheca ; the so-called basal lamina has no separate existence but is merely the common basal wall of the prostrate portions of the zooecia. Diaphragms are usually present.

The zooecia vary in height from 1 mm. to 3 mm. The superposition of several layers of zooecia in the *texturata* condition is rare. Consequently the average thickness of zoaria which are wholly in this condition is 2 mm.

Forma *irregularis* (Pl. 4, fig. 3 ; Pl. 7, fig. 1). Tangential sections show areas with regularly aligned, quadrangular zooecia, with distinct sagittate lunaria, which pass abruptly, or by mixture, into areas where the zooecia have rounded polygonal outlines and indistinct lunaria. Vertical sections show that this forma is associated with the irregular and local reduplication of zooecial layers ; thick layers show the characters of forma *typica*, thin layers those of forma *texturata* (cf. Pl. 7, fig. 1).

STRATIGRAPHICAL DISTRIBUTION. The earliest known example of the species is a specimen from the Lower Wenlock Shales at Buildwas, preserved in the Foord Collection at the British Museum (Natural History) (D.36318). It is in the *brevipora* condition, and forms an incrustation on a shell of *Meristina tumida* (Dalman). Similar specimens occur in the Upper Wenlock Shales at Walsall.

The species occurs in greatest abundance in the Wenlock Limestone, particularly in Staffordshire and at Rumney, near Cardiff. In common with other Ceramoporidae it is rare in the Wenlock Limestone of Shropshire. There is a single record of the species in the Wenlock Limestone of the Woolhope area in Herefordshire (Gardiner 1927 : 323).

Twenty-five per cent of all the Polyzoa recovered from the thin representative of the Wenlock Limestone exposed in the Ty Mawr Lane at Rumney proved to belong to this species[1]. The zoaria from this locality are all small. Most of them seem to belong to the typical forma, but the intractable ferruginous matrix with which they are encrusted makes an examination of surface features a matter of difficulty. In some specimens mesopores are very sparse (Pl. 6, fig. 4).

The great majority of the specimens of *F. interpuncta* preserved in old collections appear to have come from the shaly beds of the Wenlock Limestone at Wren's Nest and Castle Hill, Dudley, Staffordshire. Recent collecting has shown that the horizon at which they occur in greatest abundance is in the upper part of the Middle Nodular Beds. All the described formae appear to be represented at this level. The only specimen recovered from the Lower Limestone is one in the *brevipora* condition from the basement beds at Walsall. One specimen of forma *irregularis* from Dudley, preserved in the Sedgwick Museum (A5943), has a matrix which suggests derivation from the passage beds between the Upper Limestone and the Lower Ludlow.

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[1] Many of the specimens of *Favositella interpuncta* from Rumney are remarkably rich in pearls. There can be no doubt that the pearl-bearing specimens erroneously described by Sollas as *Favosites fibrosus* actually belong to this species.

A small fragmentary specimen of *Favositella* from the Aymestry Limestone of Shucknall Hill, Woolhope, Herefordshire, in the Geological Survey & Museum (57956) appears to represent a variant of this species.

REMARKS. So great is the diversity of form exhibited by *Favositella interpuncta* that some sort of subdivision of the species would seem to be desirable. An examination of an extensive series of specimens from the Wenlock beds has indicated, however, that the observed variation is continuous and not of a mutational order. The diversity of form is partly explained by the fact that different stages of astogeny are quite distinct in appearance, and partly by the marked effects on the development of this polyzoan produced by different environments.

It was therefore proposed by the author (1938) that the only way of expressing the main structural facies exhibited by the species was by applying *formal* as distinct from *varietal*, names to the several forms. The differences which the form-names indicate may be in one case developmental, in another due to the effect of a special environment, and so on. However, in the present state of our knowledge of these Polyzoa it is possible to make only very tentative correlations of this sort.

The forma *typica* seems to represent the normal form assumed by a zoarium which developed to full maturity (?gerontic stage) under constantly favourable conditions.

The forma *brevipora* is apparently the condition of zoaria which attained maturity under constant, but unfavourable conditions. In tubular Polyzoa it would seem that the length of the zooecia is not a reflexion of the rate of deposition of sediment as it is in corals, but depends mainly on the frequency of polypide-regeneration ; this in its turn being correlated with such factors as temperature, salinity and food-supply.

The forma *texturata* is the one which provides the most interesting problem. Zoaria showing this forma are so different in aspect from the typical zoaria that they were for long considered as belonging to a distinct species. In fact, judging by the evidence of museum labels, they have been generally regarded, even by palaeontologists familiar with typical *Favositella interpuncta*, as representing a species of *Ceramopora*.

The recognition of the zoaria in question as a forma of *Favositella interpuncta* resulted from the discovery that they showed features almost identical with those of a small portion of the celluliferous surface of the type-zoarium of that species. A close examination of the holotype and other typical specimens of *F. interpuncta* has shown, in fact, that wherever a new layer of zooecia has commenced to develop on the surface of a mature zoarium (i.e., wherever there has been local rejuvenation), the area of new growth shows the characters which comprise the *texturata* condition.

In other words this condition is essentially that of the neanic or sub-ephebic phases of development in *Favositella interpuncta.* Nevertheless there are reasons for regarding this condition as constituting in some cases a distinct forma.

Complete zoaria consisting of a single layer of zooecia in the *texturata* condition are of common occurrence, particularly on smooth-shelled brachiopods. The well-defined maculae which they exhibit suggest that the zoaria were fertile. The probable explanation of these forms is that they represent zoaria whose development was arrested at the sub-ephebic stage owing to certain environmental conditions.

The forma *texturata* preserves, to some extent, features of more primitive Ceramoporoid genera such as *Crepipora*; for example, the restriction of mesopores to the maculae.

Zoaria in which there has been a tendency for new layers of zooecia to develop at irregular intervals, and over small, limited areas, have a very irregular aspect which contrasts markedly with that of both forma *typica* and forma *texturata.* For such zoaria the term forma *irregularis* was proposed in 1938.

The irregular rejuvenation of the zoarial surface which tended to the production of this forma, was most probably connected with the variable character of the micro-environment. The extent to which environmental factors may have controlled growth-form in *Favositella,* may be gauged by the fact that 12 out of 13 specimens of *F. interpuncta* recovered from a single exposure in the Wenlock Limestone proved to belong to the same forma. The bed from which they came was largely composed of current-drifted shells and corals which had been accumulated in an area adjacent to a coral reef (' ball-stone ').

After further work on *Favositella interpuncta* the author found it desirable to recognize another forma, amongst the forms grouped as forma *irregularis.* The additional forma, called *intermedia,* is illustrated by Pl. 3, fig. 4. It differs from forma *irregularis* in so far as the irregularity of the surface is not due to patchy rejuvenation, but to unequal development of individual zooecia.

Favositella squamata (Lonsdale)

(Pl. 2, fig. 4 ; Pl. 3, fig. 2 ; Pl. 5, figs. 1, 3 ; Pl. 7, fig. 5 ; Pl. 8, fig. 2 ; Pl. 9, figs. 4, 5)

1839 *Discopora squamata* Lonsdale : 679, pl. 15, figs. 23, 23*a*.
1873 *Monticulipora* sp. 4 (partim) Salter : 109.
1890 *Crepipora squamata* (Lonsdale) Ulrich : 471.

LECTOTYPE (here chosen). Specimen marked *a* on slab of shelly flagstone from Wenlock Limestone, Sedgeley, figured by Lonsdale (1839, pl. 15, figs. 23, 23*a*). Geological Society Coll. 6596, Geological Survey & Museum. It is probable that Lonsdale's diagonsis of the species was wholly based on this specimen.

DESCRIPTION (Pl. 9, fig. 5). Fragment of flat laminate zoarium, 1·5 mm. thick, apparently encrusting the valve of a brachiopod. The fragment is 8 mm. long and 5 mm. wide. The surface is rather worn. The zooecia are sub-erect and contiguous. Outside the raised area the zooecial apertures are thin-walled, mainly rhomboidal and arranged in intersecting, diagonal rows ; 4 to 4½ apertures occur in an interval of

2 mm. In the subtriangular frontal half of the zooecium the apertural margin is elevated as a well-defined lunarium. The raised part of the zoarial surface is clearly a macula ; it is distinguished by the relatively large size of the zooecia and by the occurrence of numerous irregular mesopores. Mesopores have not been observed outside the macula.

External characters. Based on study of topotype material (see Pl. 2, fig. 4 ; Pl. 3, fig. 2 ; Pl. 8, fig. 2 ; Pl. 9, figs. 4, 5). Zoaria form thin encrusting sheets, generally on flat surfaces such as are provided by the valves of strophomenid brachiopods. The margins of the zoarium sometimes extend beyond the encrusted object. Free marginal expansions formed in this way have developed a coarsely wrinkled basal epitheca (Pl. 2, fig. 4). The surface of the zoarium is sometimes irregularly monticulose, but the raised areas do not invariably coincide with maculae.

The zooecial apertures are subtriangular, oval or rhomboidal. In the frontal half of the zooecium the apertural margin is raised into a prominent and rather angulated lunarium, the apex of which is often slightly overarching particularly in the maculae. The external angle of the lunarium may be acute or rounded ; in the latter case it is marked by several strong rugae or ribs which converge towards the apex. There are from 4 to 5 zooecial apertures in an interval of 2 mm. Maculae are well-marked and sometimes form low monticules ; they are superficially similar to those in *F. interpuncta* forma *texturata*, but usually show a more confused structure. The large zooecia in typical maculae have abnormally high, pointed lunarial hoods.

Mesopores are mainly small and rounded, although larger, more angular ones occur in some of the maculae. Outside the maculae, mesopores are, for the most part, only of sporadic occurrence. A notable feature of the species is the occurrence of certain circumscribed areas, distinct from normal maculae, in which minute thick-walled mesopores are so abundant that they surround the zooecial apertures. In these areas which are of irregular distribution and usually larger than the maculae, the zooecial apertures are oval or sub-pyriform, and have low, inconspicuous lunaria (Pl. 8, fig. 2).

Internal characters. Based on study of topotype material. Tangential sections (Pl. 5, fig. 3) show fairly regularly aligned, thin-walled zooecia, varying in outline from rhomboidal to sub-polygonal or sub-pyriform, and with an average diameter of 0·4 mm. The frontal end of the zooecial aperture is deeply arcuate, and lined with the lighter coloured tissue of the lunarium, which varies in form from a wide crescent to a small triangle, depending on the level at which the section has been cut. The zooecial walls are composed of the finely laminated and minutely granular tissue characteristic of the genus ; they have an average thickness of 0·028 mm. Rounded or oval mesopores, ranging in diameter from 0·08 mm. to 0·1 mm., are seen in localized areas.

In transverse sections through the sub-distal or proximal region (Pl. 5, fig. 1), the zooecia present irregularly polygonal outlines. The zooecial walls are very tenuous and tend to be somewhat flexuous. Small sub-polygonal mesopores occur mainly in the maculae. In the macular areas frequent breaks can be observed in the zooecial walls.

Vertical sections (Pl. 7, fig. 5) : in typical zoaria there are from one to four layers of zooecia. The layers vary in thickness from 1 mm. to 4 mm. The zooecial tubes arise from a thin, basal lamina, which, in the case of the lowest zooecial layers in free-growing parts of a zoarium, is usually covered by a thin epitheca. The zooecial tubes normally become almost vertical after a short prostrate phase, although in some specimens they maintain an oblique course. In the peripheral region the zooecial walls become thickened and sometimes irregularly crenulate ; short and rather thick-walled mesopores are rarely more than 0·2 mm. deep. In the peripheral zone, the walls of the mesopores and the zooecia commonly develop a ragged or loosely constructed appearance, owing to the occurrence of irregular mural pores. Diaphragms are infrequent, or absent.

OCCURRENCE. The species has been recorded only from the Wenlock Limestone of Dudley and Sedgeley. It occurs mainly in the upper part of the Middle Nodular Beds (for example at Wren's Nest), and is much rarer than *F. interpuncta*.

REMARKS. This species is easily confused with *F. interpuncta* forma *texturata*. In both the lunaria are prominent, and in both the zoarial surface tends to be divided into sharply defined sectors within which the zooecia have a constant orientation with respect to some macula. However, *F. squamata* differs from *F. interpuncta* forma *texturata* in the following respects : (i) the zooecial apertures are on the average slightly smaller and narrower ; (ii) the lunaria tend to be longer and more arcuate ; (iii) the maculae show a more confused structure ; (iv) there are circumscribed areas, apart from normal maculae, in which mesopores are abundant ; (v) the zooecial tubes are longer and more erect. The character mentioned under (iv) is an example of topomorphism.

There is no doubt that specimens of *F. squamata* showing the characters described above are normal, fully mature zoaria ; whereas the superficially similar specimens of *F. interpuncta* forma *texturata* are evidently immature, or stunted zoaria.

Favositella anoloticboides sp. nov.

(Pl. 3, figs. 1, 3 ; Pl. 5, figs. 2, 5 ; Pl. 7, figs. 3, 4 ; Pl. 9, fig. 3)

1873 *Monticulipora* sp. 6 (partim) Salter : 109.
1934 *Ceramoporella* sp., Oakley : 314, pl. 14, figs. 15, 18.

HOLOTYPE (Pl. 3, fig. 3 ; Pl. 5, figs. 2, 5 ; Pl. 7, figs. 3, 4 ; Pl. 9, fig. 3). Brit. Mus. (Nat. Hist,), D.33926, Wenlock Limestone, upper part of Middle Nodular Beds ; exposure by lime-kiln on SW side of Wren's Nest, Dudley, Staffs. The holotype is an oval, encrusting zoarium, 4–5 mm. thick, originally 40 mm. long and 27 mm. wide, attached to the surface of an '*Orthoceras*' shell.

PARATYPES. Brit. Mus. (Nat. Hist.), 8 specimens from the type locality (D.36324, D.36326–36332), and 5 others (PD.4613, D.36319, D.36325, D.36333–34) ; Sedgwick Museum, Cambridge, 2 specimens (A5964, A5899) ; National Museum of Wales, 1 specimen (G.591).

HORIZON AND LOCALITY. The species is common in the upper part of the Middle Nodular Beds of the Wenlock Limestone at Wren's Nest, Dudley. It has also been recorded from the Wenlock Limestone of Ty Mawr Lane, Rumney, near Cardiff; and from the middle beds of the Wenlock Limestone in the Coate's Farm Quarry, Presthope Road, near Much Wenlock, Shropshire.

DESCRIPTION. *External characters.* Zoaria form moderately thick encrusting sheets on cephalopod shells, corals, stromatoporoids, and more rarely on brachiopod shells. Where the zoarium extends beyond the encrusted body, the basal surface becomes enveloped by a thin, wrinkled epitheca. The surface of the zoarium is usually somewhat uneven, but there are no definite macular elevations or depressions. The zooecia are relatively thick-walled and radiate from macular centres spaced at intervals of about 5 mm. Each has a thin, horse-shoe shaped lunarium, the edges of which bear minute, acanthopore-like granules. The zooecial apertures vary in outline; they tend to be roughly elongate-oval or sub-pyriform, but a slight constriction of the walls at the ends of the lunarial loop gives the apertures the form of a key-hole. Locally the apertures become meandrine owing to the coalescence of some of the zooecia.

Internal characters. In tangential sections (Pl. 5, figs. 2, 5) the majority of the zooecia present slightly 'waisted', oval outlines, with an average major axis of 0·45 mm. and an average minor axis of 0·27 mm. The outlines of some zooecia appear geniculate owing to a slight declination of the axis of the lunarium relative to the axis of the anterior part of the aperture. As seen in section, the lunarium is a narrow band of light-coloured tissue, varying in form from a semi-circle to a three-quarter circle, and constituting the frontal third of the zooecial wall. In sections of well-preserved specimens it is possible to see 9–12 acanthopore-like granules, or tubules, within the lunarium (Pl. 5, fig. 2). These appear as pellucid spots with an average diameter of 0·02 mm. They are rather irregularly placed and their margins occasionally project into the zooecial cavity. The zooecial walls vary considerably in thickness; the frontal wall, formed by the lunarium, has an average thickness of 0·025 mm., but elsewhere the walls may attain a thickness of as much as 0·05 mm. Sub-polygonal mesopores, varying in diameter from 0·1 mm. to 0·3 mm., are abundant and practically surround the zooecia. Gaps in the walls of both mesopores and zooecia are common and lead locally to meandrine outlines.

Vertical sections (Pl. 7, figs. 3, 4) usually reveal a single layer of zooecia; more rarely there are two superimposed layers. The thickness of a zooecial layer varies from 2 mm. to 5 mm. The zooecial tubes arise from a thin basal lamina which is epithecated in the case of free-growing expansions. The zooecia pass through a brief prostrate phase and then rise vertically; they have irregularly crenulate walls in which occasional breaks may be observed. The walls are thickened throughout the mature zone by auxiliary ectocyst. Thin diaphragms, concave upwards, occur fairly frequently, but without any regular spacing, the intervals separating them varying from one to three tube-diameters. Mesopores are intercalated between the zooecia at the point where they become vertical, and persist throughout the mature zone. They are loosely moniliform, or in some cases definitely vesicular in character

(Pl. 7, fig. 4). Diaphragms similar to those in the zooecia are usually seen in some of the mesopores. The walls of the mesopores, like those of the zooecia, are locally broken by numerous gaps, a tendency particularly marked in macular centres.

The wall-tissue is less laminar and more granulated than in the two preceding species.

REMARKS. This species provides an interesting problem in systematics. It differs from all previously described species of *Favositella* in the isolation of its zooecia by mesopore tissue and in the presence of acanthopore-like granules in its lunaria. In the first of these characters, as in its habit, it recalls species of *Ceramoporella*. On the other hand, the lunarial structures as seen in tangential sections are reminiscent of the tubules found in the lunaria of the Ordovician genus *Anolotichia*.

However, in *Anolotichia* the maximum number of tubules in a lunarium appears to be seven, whereas in the present form there are often as many as twelve. Furthermore, in vertical section there is no indication that the tubules in this species have either the extension or the tabulated structure characteristic of those in *Anolotichia*. They can scarcely be regarded as tubules at all, and seem to have much more in common with the granules found in the walls of certain species of *Ceramoporella* (e.g. *C. granulosa* Ulrich 1890 : 466). This fact, considered in conjunction with the abundance of the mesopores, at first suggested that the correct reference of this polyzoan was to *Ceramoporella*. More detailed investigation showed, however, that the zooecial walls are frequently perforated by irregular pores—a feature, which has never been observed in species of *Ceramoporella*. Moreover, in many specimens the mesopores are found to exhibit the loose, vesicular character generally associated with those of *Favositella*. These and more general considerations finally left no doubt in the author's mind that this polyzoan was, in fact, like the commoner pearl-bearing forms, a species of *Favositella*, but one with a superficial resemblance to *Anolotichia* on the one hand, and to *Ceramoporella* on the other.

Although there is no doubt that this polyzoan agrees more closely with *Favositella* than with any other known genus of Ceramoporidae, the fact that it differs from all previously described species of that genus in having acanthopore-like granules in the frontal wall of the zooecium might have been taken as sufficient reason for regarding it as the type of a new genus or sub-genus. It is considered, however, that the wiser course is to include it in *Favositella*, at any rate until there is more proof that such acanthopore-like granules are of phylogenetic significance. The sporadic appearance of these or similar structures in isolated species of distantly related stocks suggests that they are of no more than specific importance. For example, acanthopore-like granules can be detected in the zooecial walls of *Crepipora lunatifera* Bassler (1911 : 88, fig. 27*d*), but have not been observed in other species of that genus. Again, analogous granules occur in the zooecial walls of some species of *Ceramoporella* (e.g. *C. granulosa* Ulrich 1890 : 466), but not in others. Tabulated lunarial tubules fall into a different category, since they are only found in species with a number of important characters in common, and their presence is therefore justifiably taken to indicate membership of a single generic group, to which the name *Anolotichia* has been given.

Favositella gotlandica sp. nov.

(Pl. 2, fig. 5; Pl. 5, figs. 4, 6; Pl. 9, figs. 1, 2)

HOLOTYPE. Brit. Mus. (Nat. Hist.), D. 33919; and D.33923 (thin-section); Upper Silurian (Gotlandian), Mülde-margelsten (=Lower Ludlow), Mülde Tile-factory, near Fröjel, Gotland. It consists of an encrustation on a shell of *Meristina tumida* (Dalman).

DESCRIPTION. Zoarium thin and encrusting; surface slightly uneven. Zooecial apertures regularly aligned, thin-walled and sharply rhomboidal in outline, with small, sharply elevated lunaria. On the average there are 4 zooecia in 2 mm. The zooecial tubes are sub-erect and contiguous. Small mesopores, having the appearance of punctations, occur sporadically at wall-intersections. Maculae, although sometimes slightly raised, are relatively inconspicuous; they are mainly recognizable by the local abundance of mesopores.

In sections the zooecial walls are remarkable for their uniform thinness throughout. Their average thickness is 0·02 mm. (compared with 0·05 mm. in the mature zone of *F. interpuncta* forma *typica*; 0·035 mm. in the forma *texturata* of that species; and 0·028 mm. in *F. squamata*).

In tangential section the zooecia show rhomboidal outlines with an average major axis of 0·6 mm., and an average minor one of 0·35 mm. in length. The frontal end of the zooecium is narrowly rounded and lined by an extremely narrow, crescentic lunarium which can only be observed in sections which pass very close to the surface. Mesopores are initially quadrangular, but their lumen has usually become rounded through the growth of auxiliary ectocyst.

The vertical section shows a single zooecial layer with an average thickness of 0·7 mm. The zooecial tubes curve obliquely upwards after a brief prostrate stage. The actual apertures are sub-direct. Mesopores are simple, short, and widen upwards. Small gaps in the zooecial walls can be observed in parts of the zoarium, and indicate the presence of mural openings. Diaphragms have not been observed.

REMARKS. This species is closely related to *F. squamata* (Lonsdale) from the Wenlock Limestone, the two resembling one another in the rhomboidal form of the zooecial apertures and in the comparative thinness of the zooecial walls. The present species is mainly distinguished from *F. squamata* by the smallness of its lunaria, by the more regular shape of the zooecial apertures, and by the curving obliquity of its zooecial tubes as seen in vertical section.

The horizon from which the holotype was collected is in Lindström's Division *c* of the Gotlandian formation; that is the Mülde-margelsten, which has been correlated by Hede (1921 : 87) with the Lower Ludlow beds of this country.

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PLATE 1

FIG. 1. Section of spherule with nucelus resembling polyzoan 'secondary embryo' (cf. Borg 1926 : pl. 14, 90). Taken from section of ***Favositella interpuncta*** (Quenstedt). ×420. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33702.

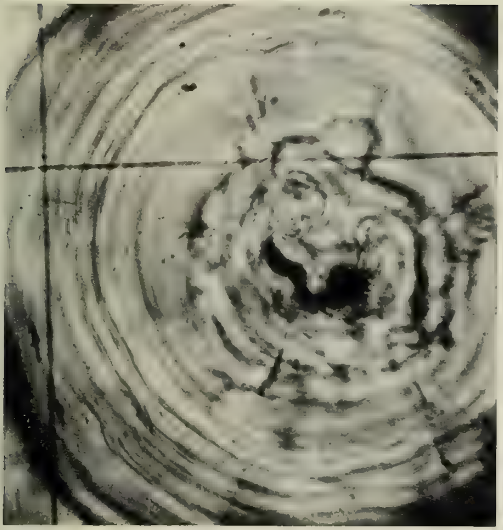
FIG. 2. Group of polyzoan pearls. ×50 (approx.). Extracted from specimen of ***Favositella interpuncta*** (Quenstedt) from Wenlock Limestone; Rumney. Brit. Mus. (N.H.) D.36473.

FIG. 3. ***Favositella interpuncta*** (Quenstedt). Vertical section showing typical position of pearl-like spherules within a zooecium. ×60. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33702.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Inferior aspect of Fig. 5, showing shell of *Loxonema* over which the polyzoan has grown.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Lateral aspect of 'drumlinoid' zoarium. ×1. Wenlock Limestone; Dudley. Holcroft Coll. 370, Geol. Dept., Birmingham University.

FIG. 6. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Lateral aspect of tumular zoarium with conical elevation, showing monticulose maculae; originally figured by Etheridge & Foord (1884, pl. 17, fig. 1). ×1. Wenlock Limestone; Dudley (erroneously catalogued as from Benthall Edge). Brit. Mus. (N.H.) R.1186.



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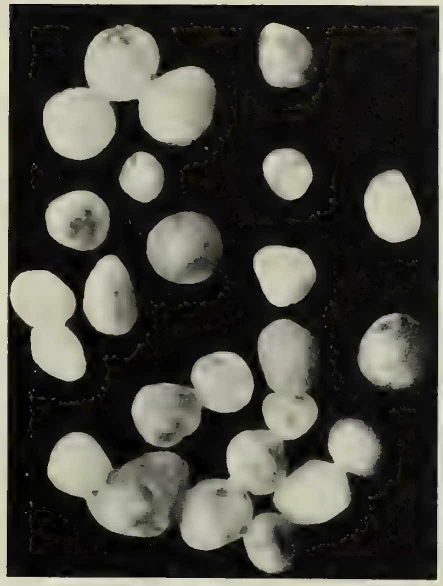

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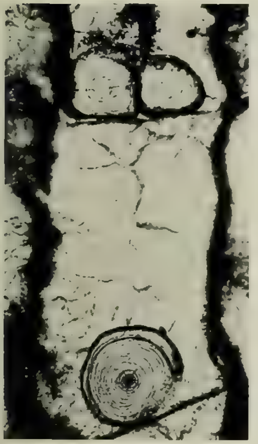

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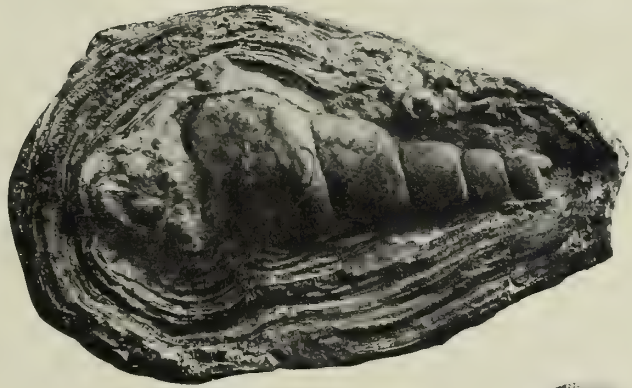

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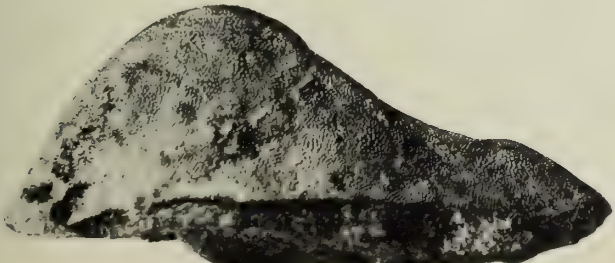

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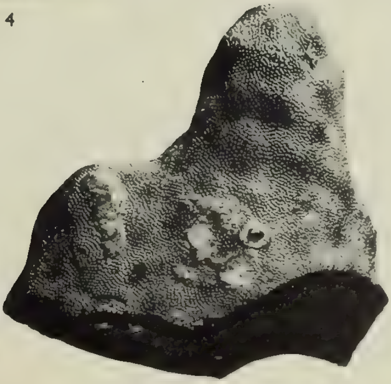

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PLATE 2

FIG. 1. ***Favositella interpuncta*** (Quenstedt). Lectotype. Lateral aspect. ×2. Wenlock Limestone; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Vertical section through 'drumlinoid' zoarium showing hollow base. ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33701.

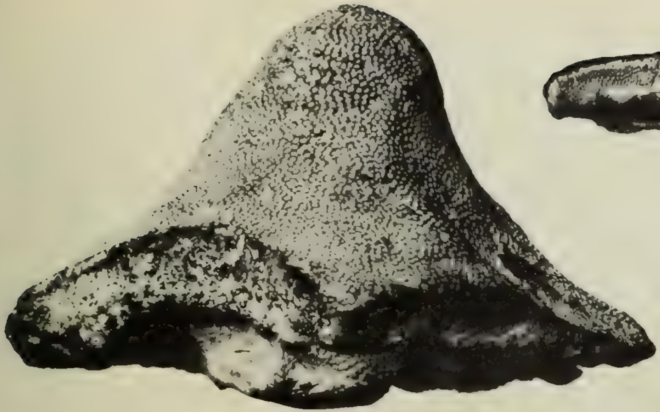
FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Large tumular zoarium. ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.36340.

FIG. 4. ***Favositella squamata*** (Lonsdale). Inferior surface of zoarium showing epithecated marginal expansion. ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33711.

FIG. 5. ***Favositella gotlandica*** sp. nov. Holotype, zoarium encrusting shell of *Meristina tumida* (Dal.). ×1. Mülde-margelsten; nr. Fröjel, Gotland. Brit. Mus. (N.H.) D.33919.

FIG. 6. ***Favositella interpuncta*** (Quenstedt). Lectotype. Inferior surface showing corrugated epitheca. ×2. Wenlock Limestone; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

FIG. 7. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Zoarium encrusting shell of *Meristina tumida* (Dalman). ×3/2. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.



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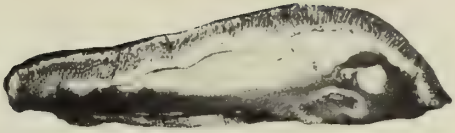

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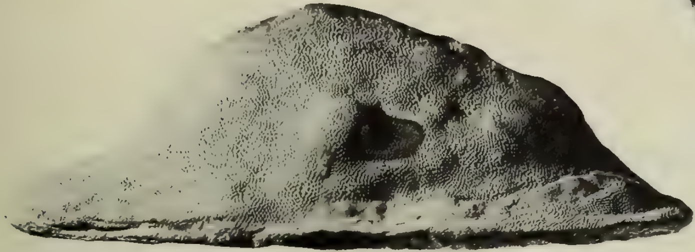

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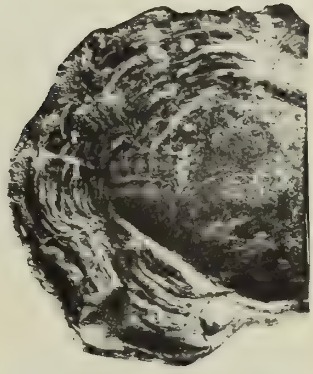

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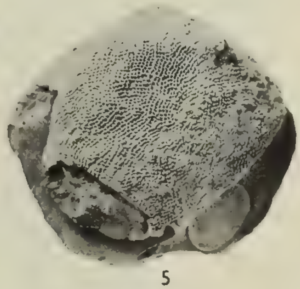

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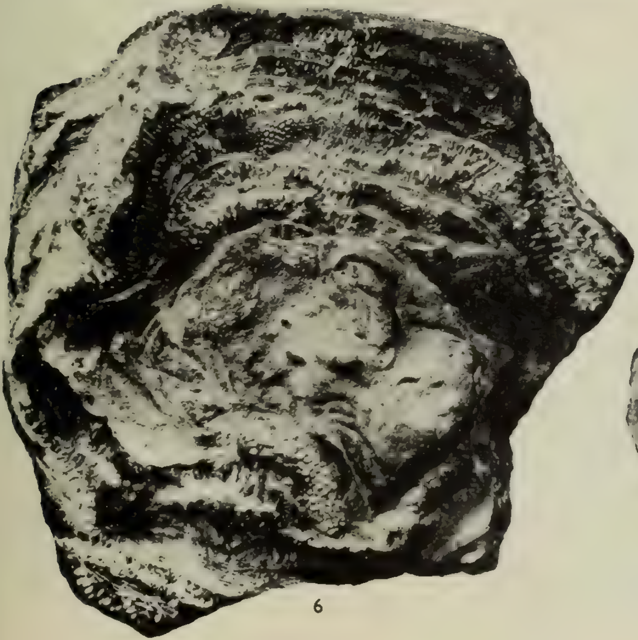

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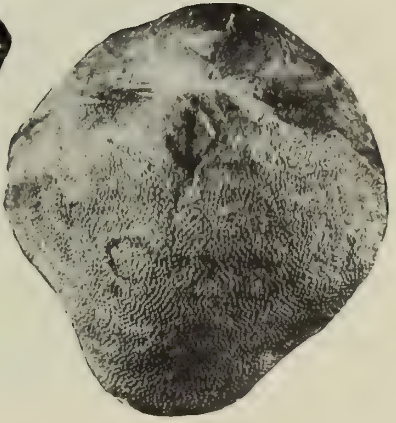

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PLATE 3

Fig. 1. ***Favositella anoloticholdes*** sp. nov. Paratype ×4·5. Wenlock Limestone; Coate's Farm Quarry, Much Wenlock. Brit. Mus. (N.H.) D.36325.

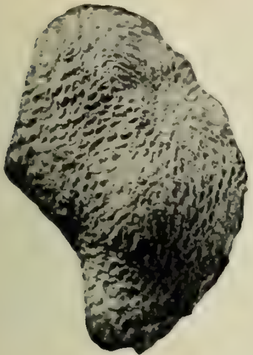
Fig. 2. ***Favositella squamata*** (Lonsdale). Celluliferous surface of zoarium. ×2. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) R.2592.

Fig. 3. ***Favositella anoloticholdes*** sp. nov. Holotype. ×2. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926*a*.

Fig. 4. ***Favositella interpuncta*** (Quenstedt) forma ***intermedia***. Zoarium encrusting ramose coral. ×1·5. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.36339.

Fig. 5. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Zoarium encrusting shell of *Meristina tumida* (Dalman.). ×1. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33715.

Fig. 6. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Tumular zoarium with several hollow maculae. ×2. Wenlock Limestone; Dudley. Holcroft Coll. 570, Geol. Dept., Birmingham University.



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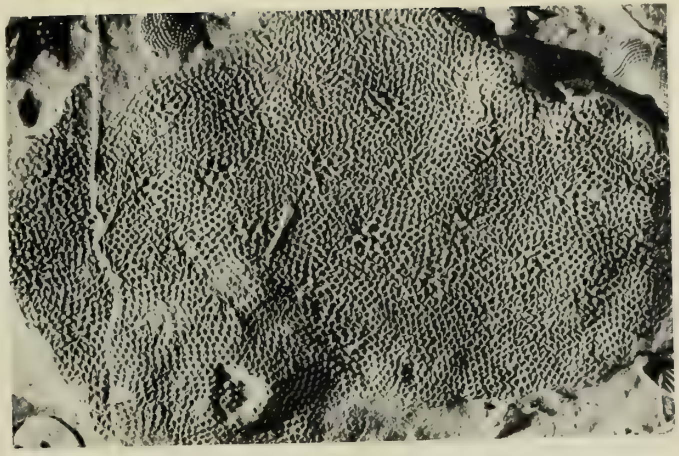

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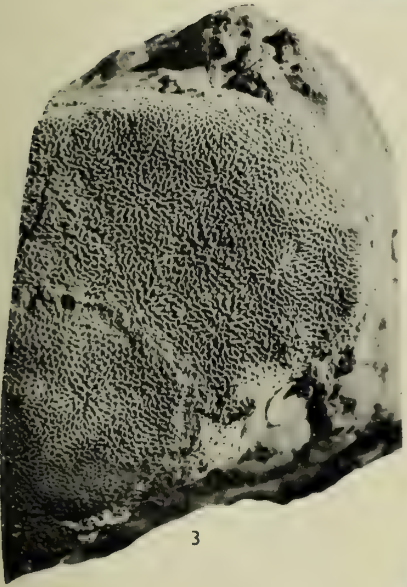

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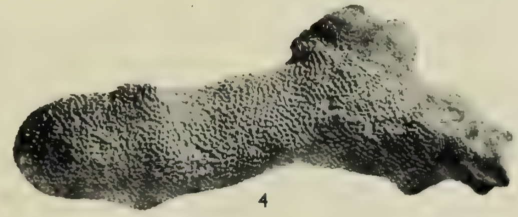

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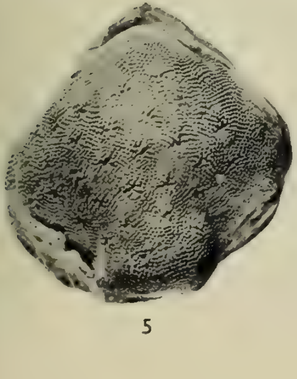

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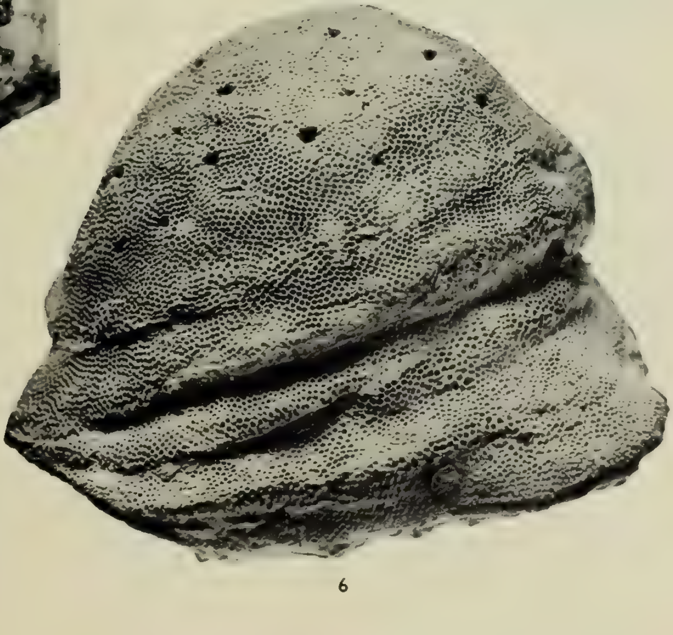

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PLATE 4

FIG. 1. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Tangential section. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33697.

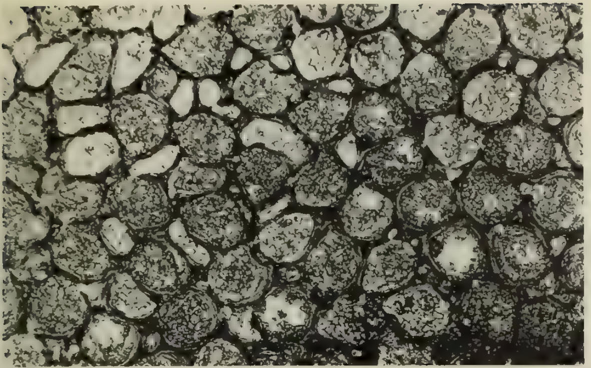
FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Tangential section. ×22. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.

FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***irregularis***. Tangential section showing transition from immature zone, with diagonal rows of quadrangular zooecia showing sagittate lunaria, to mature zone with rounded-polygonal zooecia of the typical forma. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33720.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Tangential section showing sagittate lunaria. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33672.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Tangential section passing through macular area in which numerous mural openings are evident. ×22. Wenlock Limestone; Ty Mawr Lane, Rumney. Brit. Mus. (N.H.) D.33686.

FIG. 6. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Tangential section. ×22. Wenlock Limestone, Basement beds of Lower Limestone; Daw End railway-cutting, Walsall. Brit. Mus. (N.H.) D.36337.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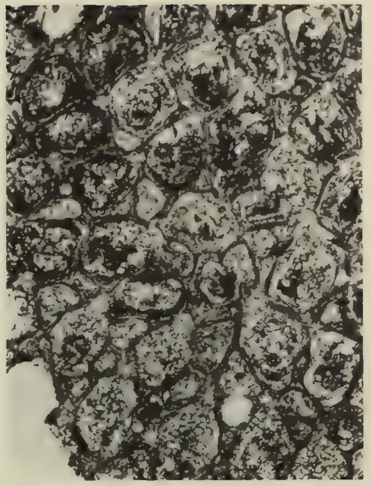
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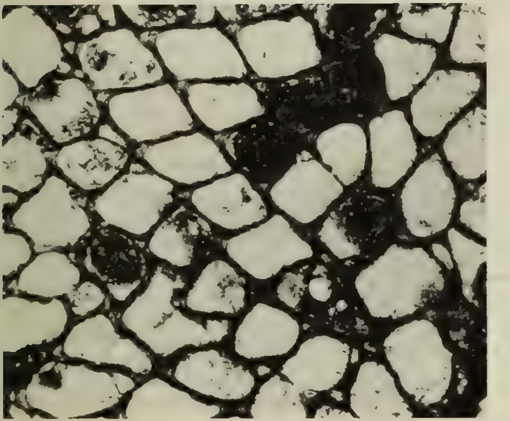
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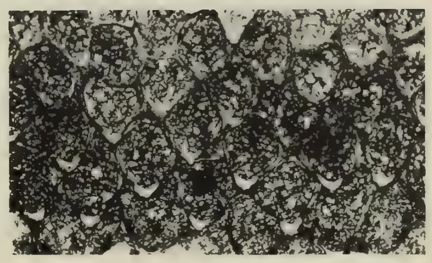
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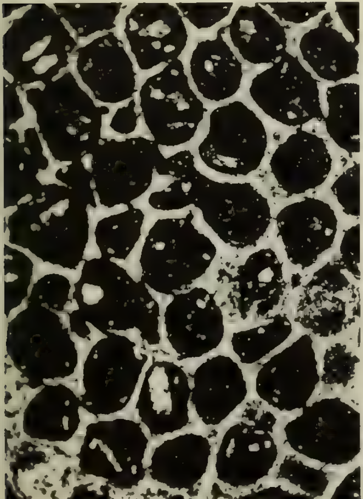
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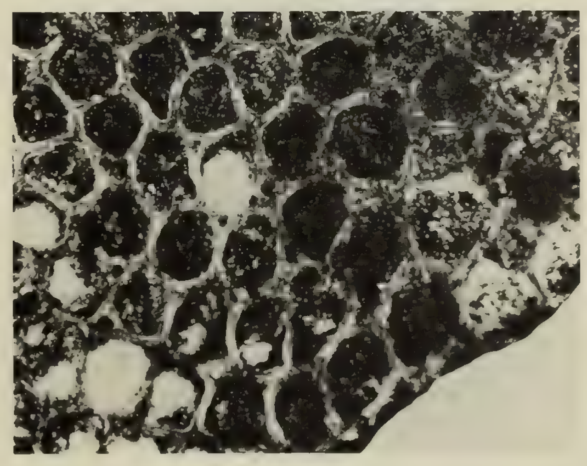
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PLATE 5

Fig. 1. ***Favositella squamata*** (Lonsdale). Transverse section through sub-ephebic level of zoarium. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33718.

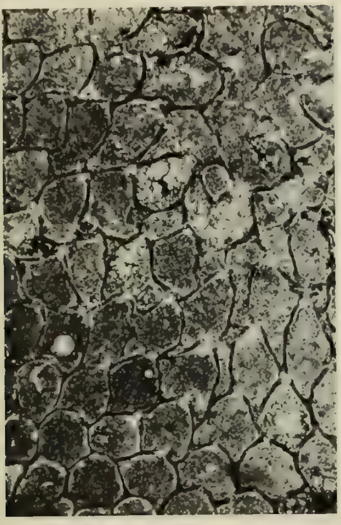
Fig. 2. ***Favositella anoloticoides*** sp. nov. Thin tangential section of holotype, showing acanthopore-like granules in lunarium. ×40. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926*c*.

Fig. 3. ***Favositella squamata*** (Lonsdale). Tangential section showing arcuate form of lunaria. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33714.

Fig. 4. ***Favositella gotlandica*** sp. nov. Sagittal section of holotype, showing narrow lunarium (l) and obliquely curving zooecia. ×22. Upper Silurian (Gotlandian) ; nr. Fröjel, Gotland. Brit. Mus. (N.H.) D.33923.

Fig. 5. ***Favositella anoloticoides*** sp. nov. Tangential section of holotype. ×30. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926.

Fig. 6. ***Favositella gotlandica*** sp. nov. Transverse section of holotype, showing dahllite pearls within the zooecia. ×30. Upper Silurian (Gotlandian); nr. Fröjel, Gotland. Brit. Mus. (N.H.) D.33923.



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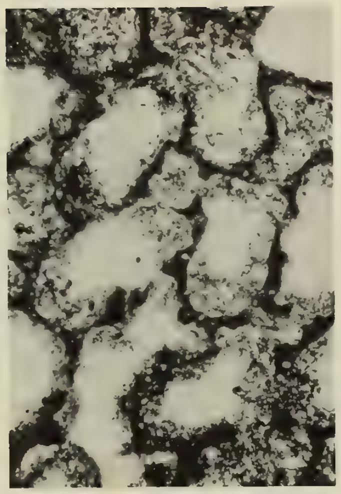

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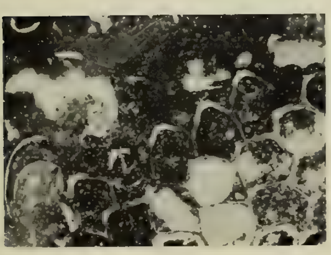

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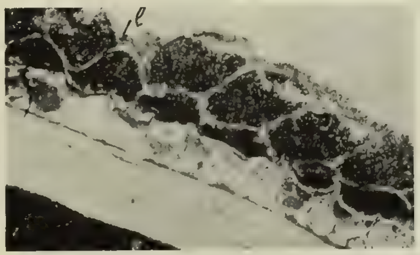

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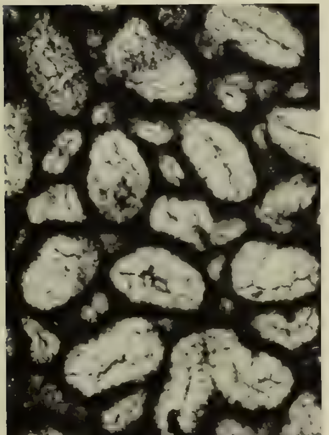

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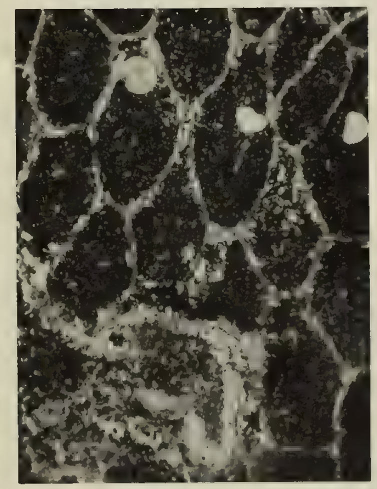

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PLATE 6

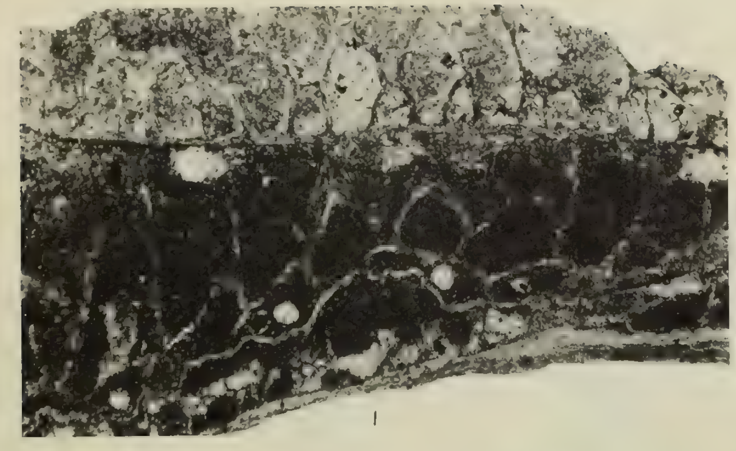
FIG. 1. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Vertical section showing two superimposed layers of zooecia. ×22. Wenlock Limestone, Basement beds of Lower Limestone ; Daw End railway-cutting, Walsall. Brit. Mus. (N.H.) D.36338.

FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***brevipora***. Vertical section showing two layers of zooecia. ×22. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.

FIG. 3. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Vertical section cutting prostrate bases of zooecia longitudinally. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33689.

FIG. 4. ***Favositella interpuncta*** (Quenstedt) forma ***typica***? Vertical section showing contiguous zooecia with crenulate walls ; a pearl is visible on bottom right of mid-line. The upper surface of the section is on the left. ×22. Wenlock Limestone ; Ty Mawr Lane, Rumney. Brit. Mus. (N.H.) D.33696.

FIG. 5. ***Favositella interpuncta*** (Quenstedt) forma ***typica***. Vertical section through mature zone. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33696.



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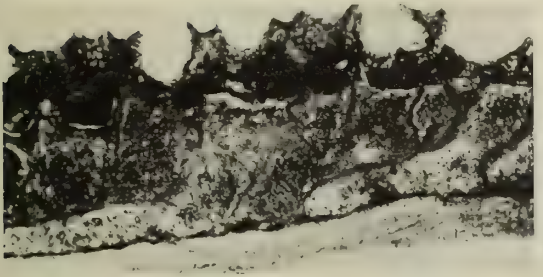

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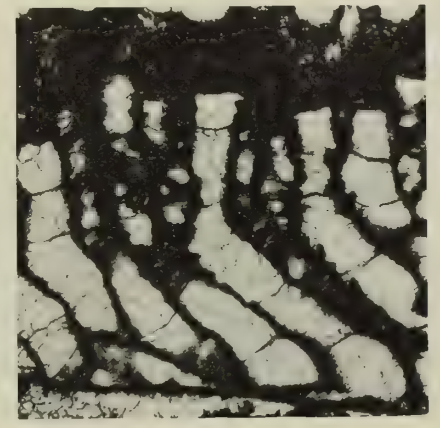

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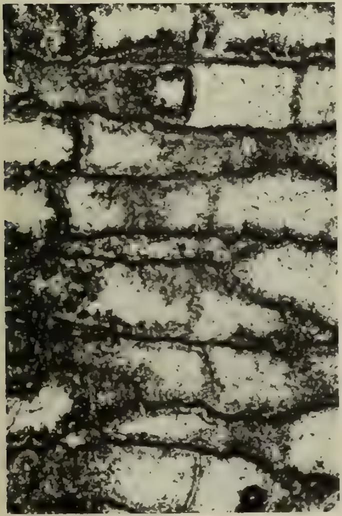

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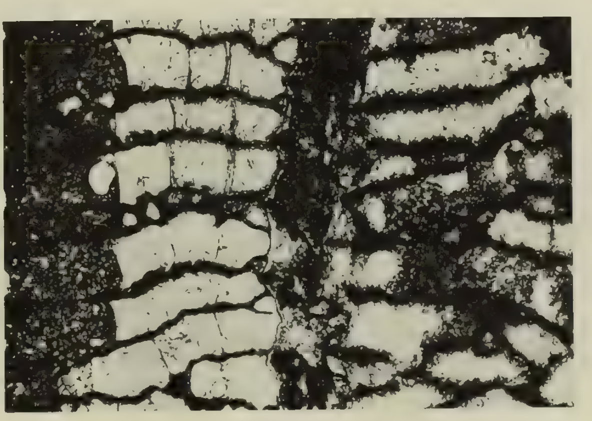

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PLATE 7

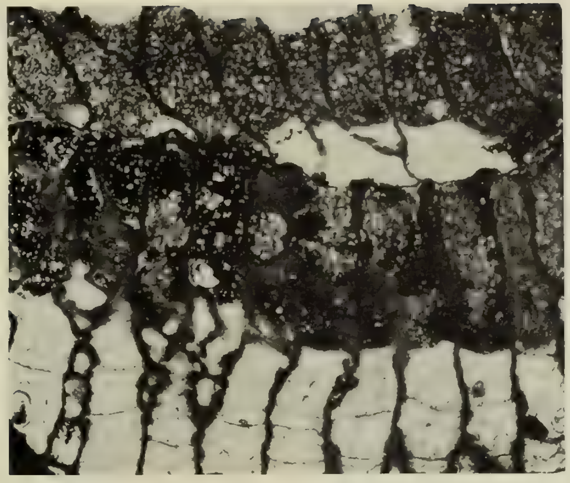
FIG. 1. ***Favositella interpuncta*** (Quenstedt) forma ***irregularis***. Vertical section of zoarium showing local rejuvenation of zoarial surface: layer of zooecia in ***texturata*** condition (cf. Pl. 7, fig. 2) overlying normally matured zooecia. ×20. Wenlock Limestone; Dudley. Sedgwick Museum, Cambridge. A5891*d*.

FIG. 2. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Vertical section. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33670.

FIG. 3. ***Favositella anoloticholdes*** sp. nov. Vertical section of holotype, showing characteristic mesopores. ×30. Wenlock Limestone, Middle Nodular Beds; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926*d*.

FIG. 4. ***Favositella anoloticholdes*** sp. nov. Vertical section of holotype, showing unusually vesicular mesopores. ×22. Brit. Mus. (N.H.) D.33926*b*.

FIG. 5. ***Favositella squamata*** (Lonsdale). Vertical section through double-layered zoarium; in the lower layer the prostrate portions of the zooecia are cut longitudinally, in the upper, transversely. ×20. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33712.



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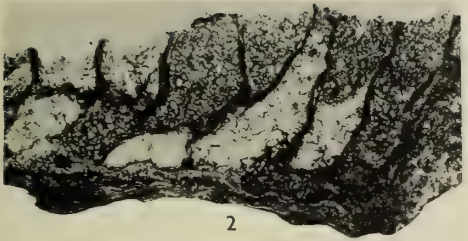

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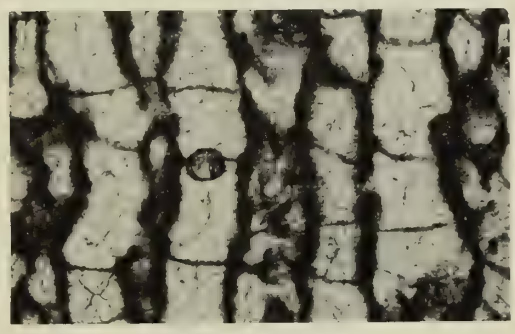

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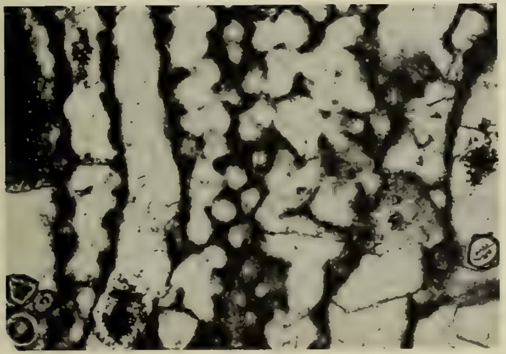

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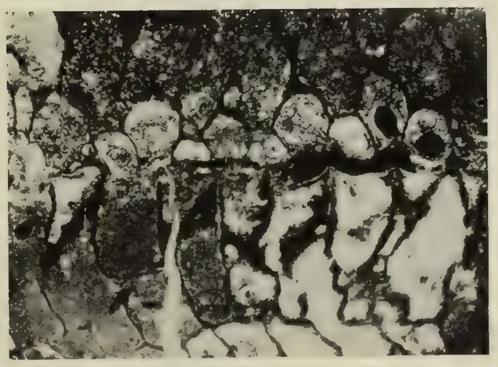

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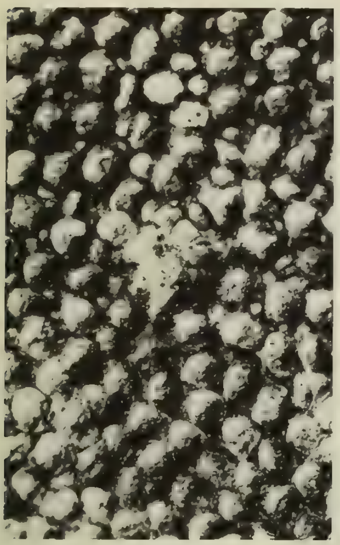
PLATE 8

Fig. 1. ***Favositella interpuncta*** (Quenstedt). Lectotype. Typical portion of celluliferous surface showing rounded thick-walled zooecial apertures; hollow stellate macula in centre. × 10. Wenlock Limestone ; Dudley. Geolog.-Paläontologisches Institut, Tübingen.

Fig. 2. ***Favositella squamata*** (Lonsdale). Celluliferous surface of a typical zoarium; area with abundant mesopores and repressed lunaria in top right-hand corner. × 8. Wenlock Limestone; Dudley. Holcroft Coll. 517, Geol. Dept., Birmingham University.

Fig. 3. ***Favositella interpuncta*** (Quenstedt) forma ***texturata***. Celluliferous surface. × 10. Wenlock Limestone; Dudley. Brit. Mus. (N.H.) D.33670.

Fig. 4. ***Favositella interpuncta*** (Quenstedt). Lectotype. Rejuvenated portion of celluliferous surface showing thin-walled, quadrangular zooecia with thin, hood-like lunaria; a macula is visible at the centre. × 10. Wenlock Limestone ; Dudley. Geolog.-Paläontologisches Institut, Tübingen.



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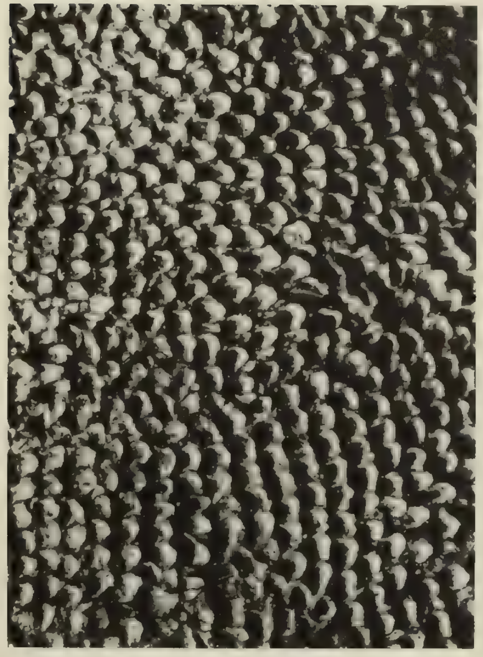

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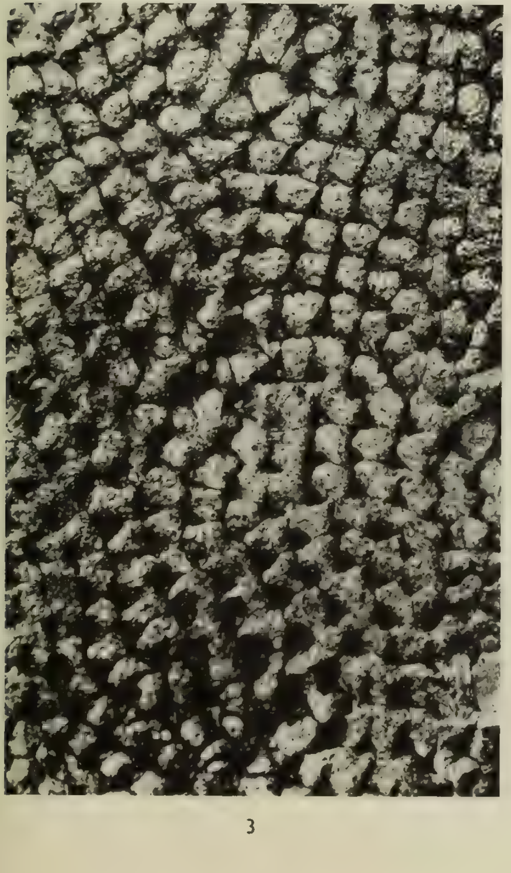

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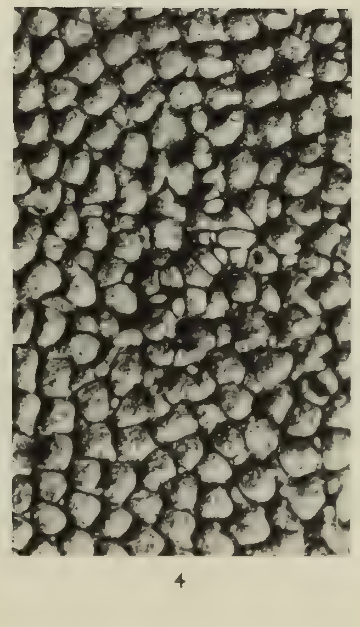

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PLATE 9

FIG. 1. **Favositella gotlandica** sp. nov. Celluliferous surface of holotype. ×6. Upper Silurian (Gotlandian) ; nr. Fröjel, Gotland. Brit. Mus. (N.H.) D. 33919.

FIG. 2. **Favositella gotlandica** sp. nov. Ditto. ×6.

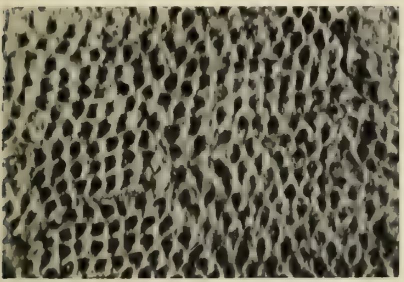
FIG. 3. **Favositella anoloticholdes** sp. nov. Celluliferous surface of holotype. ×5. Wenlock Limestone, Middle Nodular Beds ; Wren's Nest, Dudley. Brit. Mus. (N.H.) D.33926.

FIG. 4. **Favositella squamata** (Lonsdale). Celluliferous surface. ×6. Wenlock Limestone; Dudley. Holcroft Coll. 182, Geol. Dept., Birmingham University.

FIG. 5. **Favositella squamata** (Lonsdale). Celluliferous surface of lectotype. ×4. Wenlock Limestone; Dudley. Geol. Soc. Coll. 6596, Geol. Surv. Mus.

FIG. 6. **Favositella interpuncta** (Quenstedt) forma **typica**. Portion of surface of Pl. 3, fig. 6, enlarged to show hollow maculae (cf. brood-chambers in *Neofungella* ; Borg 1933 ; pl. 2 fig. 4). Wenlock Limestone ; Dudley. Holcroft Coll. 570, Geol. Dept., Birmingham University.

FIG. 7. **Favositella interpuncta** (Quenstedt) forma **brevipora**. Celluliferous surface of zoarium (on reverse aspect of specimen illustrated in Pl. 2, fig. 7). ×4. Wenlock Limestone; Dudley. Greenough Coll. 028, Geol. Dept., Univ. College, London.



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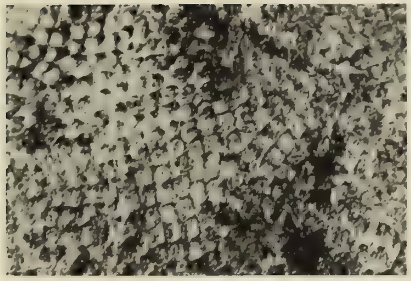

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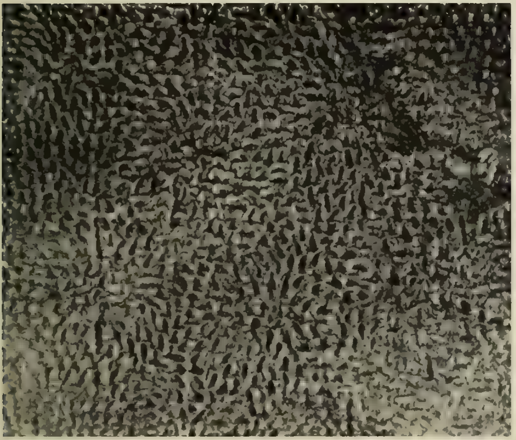

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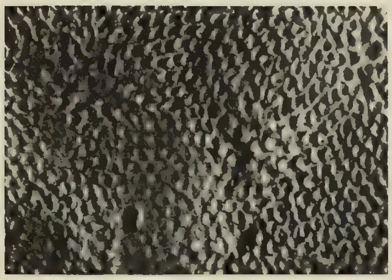

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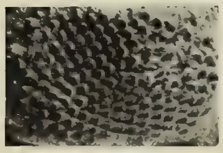

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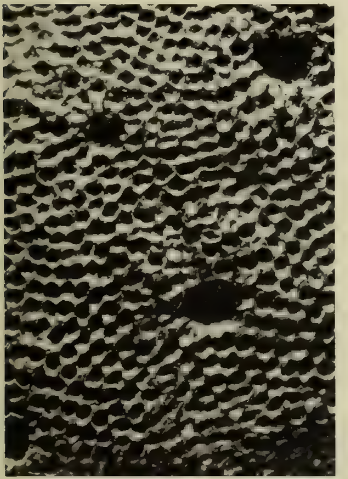

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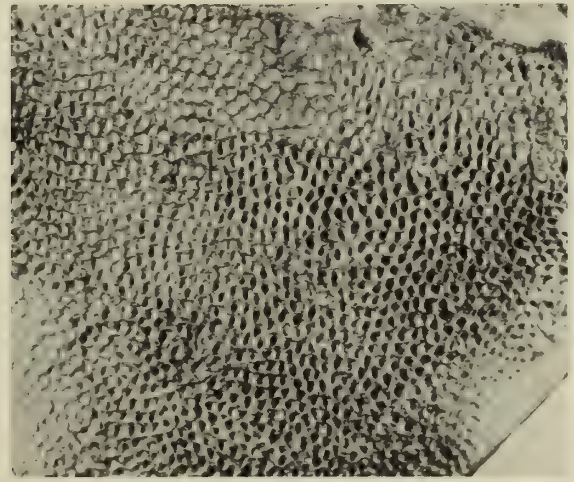

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NATURAL HISTORY

THE BATHONIAN UPPER ESTUARINE SERIES OF EASTERN ENGLAND

PART I: OSTRACODA

R. H. BATE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 14 No. 2
LONDON: 1967

8 FEB 1
NATURAL HIS

THE BATHONIAN UPPER ESTUARINE SERIES OF EASTERN ENGLAND

PART I: OSTRACODA

BY

RAYMOND HOLMES BATE

Pp. 21–66; 22 *Plates*; 1 *Text-figure*

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THE BATHONIAN UPPER ESTUARINE SERIES OF EASTERN ENGLAND

PART I: OSTRACODA

By R. H. BATE

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SYNOPSIS

Twenty-nine species of Ostracoda, of which 18 are new, are described from the Bathonian Upper Estuarine Series of Eastern England. Of this ostracod fauna two genera, *Belekocytheridea* and *Platycythere*, and two subgenera, *Eoschuleridea* and *Mediodentina* are new. A palaeoecological study of the ostracod faunas indicates an alternation throughout the succession of marine and freshwater conditions. Of the two new genera, *Belekocytheridea* inhabits a brackish water environment and *Platycythere* a marine to brackish water environment. Of the two new subgenera, *Eoschuleridea* is marine whilst *Mediodentina* is euryhaline, ranging from marine through brackish to almost freshwater conditions.

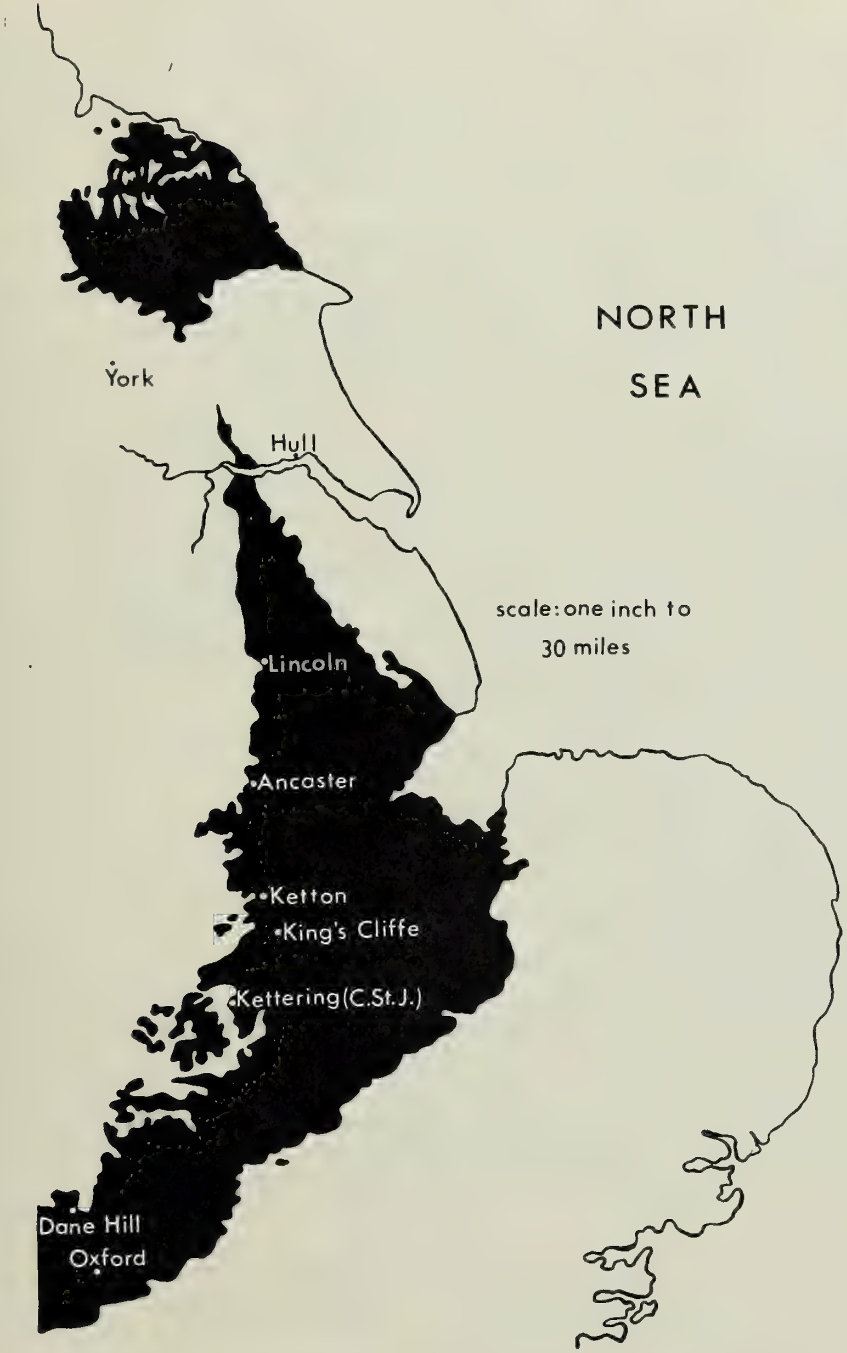

NORTH
SEA
York
Hull
scale: one inch to
30 miles
Lincoln
Ancaster
Ketton
King's Cliffe
Kettering (C.St.J.)
Dane Hill
Oxford

FIG. 1. Outcrop of Middle and Upper Jurassic Rocks in Eastern and Northeastern England with localities sampled within the Upper Estuarine Series shown.

I. INTRODUCTION AND ACKNOWLEDGMENTS

STRETCHING from North Lincolnshire to the borders of Oxfordshire is a narrow strip of marine and freshwater clays, with some thin limestones, showing evidence of deposition in shallow water. These beds, known as the Upper Estuarine Series, underlie the rubbly limestones of the Bathonian Great Oolite Limestone and with a marked unconformity overlie the Bajocian Lincolnshire Limestone. They form the basal Bathonian sediments in the area.

The absence of ammonites from the Upper Estuarine Series makes the dating of these sediments rather difficult. However, mapping and the examination of the invertebrate faunas suggests that they may be equivalent to the Hampen Marly Beds of further south. Certainly the ostracod faunas would not, at this stage, disagree with this. If this correlation is to be regarded as correct, the Upper Estuarine Series would be Middle Bathonian in age and belong to the zone of *Tulites subcontractus* (Morris & Lycett).

Although of shallow water origin, there is evidence to suggest that these beds are not estuarine deposits in the strictest sense. Dr. C. J. Aslin of the University of East Anglia has for some time now been working on the stratigraphical and sedimentological problems of the Upper Estuarine Series, and it was he who made available his large collection of ostracods which form the basis of the present paper.

The sections from which the ostracods were obtained occur in large quarries where the Upper Estuarine Series represents the overburden. The continual cutting back of these sediments makes it impossible to maintain a permanent section. The quarries are located as follows (see Text-fig. 1):

Kings Cliffe—TL/012966.
Ancaster (Thompson's Pit)—SK/992409.
Ketton (Portland Cement Quarry)—SK/972057–9.
Cranford St. John (Kettering)—SP/926764.
Dane Hill—SP/465273.

It should be noted that in some cases the quarries are sited a mile or so from the town whose name they bear.

The morphological terms used in the present paper are taken from Sylvester-Bradley (1956), Moore (1961) and Bate (1963). All the ostracods described in the text have been deposited in the collections of the Palaeontology Department, British Museum (Natural History).

I should like to record my grateful thanks to Dr. H. J. Oertli, S.N.P.A., Pau, France, and to Dr. H. Malz, Senckenberg Museum, Frankfurt, Germany, for the loan of material which proved invaluable for comparison with the present fauna. Mr. S. H. Eagar printed the photographs originally taken by myself.

II. SYSTEMATIC DESCRIPTIONS

The beds from which the ostracods were obtained are identified by a letter and refer to beds described by Aslin (in press).

Order PODOCOPIDA Müller 1894

Suborder PODOCOPINA Sars 1866

Superfamily **CYPRIDACEA** Baird 1845

Family **PARACYPRIDIDAE** Sars 1923

Genus ***PARACYPRIS*** Sars 1866

Paracypris terraefullonica (Jones & Sherborn)

(Pl. 1, figs 1–6)

1888 *Macrocypris terrae-fullonicae* Jones & Sherborn : 252, pl. 5, figs. 3*a–c*.
1888 *Macrocypris horatiana* Jones & Sherborn : 252, pl. 5, figs. 2*a–c*.

DIAGNOSIS. *Paracypris* with elongate carapace, posteriorly acuminate. Anterior rounded. Ventral margin almost straight in the larger left valve, more strongly concave in right. Dorsal margin arched with antero-dorsal slope tending to be slightly concave, more noticeably so in right valve. Shell surface smooth. Anterior and posterior vestibules well developed. Radial pore canals branching.

LECTOTYPE. Selected here, I.1875, left valve, from the Blue Fullers-earth clay; Midford near Bath, figured Jones & Sherborn 1888, pl. 5, figs. 3*a–c*.

OTHER MATERIAL. I.1874, right valve, from the Blue Fullers-earth clay; Midford near Bath, figured Jones & Sherborn 1888, pl. 5. figs. 2*a–c*. Io.2250–58, from the Upper Estuarine Series, beds M, R & S, Kings Cliffe; base of bed H: Ketton and bed I, Kettering.

DESCRIPTION. **Carapace** elongate, subreniform, rounded anteriorly, acuminate posteriorly. Dorsal margin arched, convex in the right valve, almost straight, sloping posteriorly in the left. Cardinal angles rounded. Antero-dorsal slope tends to be slightly concave, particularly just behind the anterior margin, a situation more noticeable in the right valve. Ventral margin almost straight in the left valve, concave medially in the right. Greatest height of carapace in anterior third in the left valve, almost median in the right. Greatest length below mid-point; greatest width median. Shell surface smooth. Left valve larger than the right which it overlaps along the ventral, postero-dorsal and antero-dorsal slopes. Posteriorly the left valve slightly over-reaches the right whilst anteriorly the right valve over-reaches the left. **Hinge** consists of a simple groove in the left valve into which the dorsal edge of the right valve fits. **Inner margin** and **line of concrescence** do not coincide terminally, prominent **vestibules** being produced. Anteriorly the vestibule is broad whilst posteriorly more narrow, extending along the postero-ventral margin of the inner part of the valve up to the centre of the median incurvature. **Radial pore canals** not clearly observed, but appear to be few in number and antero-ventrally can be seen to be branching. Three centrally situated oval **muscle scars** can be distinguished in the lectotype with a fourth situated behind.

DIMENSIONS. Lectotype. I.1875, left valve, length 0·60 mm., height 0·28 mm. Other material. I.1874, right valve, length 0·58 mm., height 0·26 mm. Io.2250, carapace, length 0·65 mm., height 0·31 mm., width 0·27 mm. Io.2251, right valve length 0·65 mm., height 0·31 mm. Io.2255, right valve, length 0·65 mm., height 0·31 mm. Io.2256, carapace, length 0·60 mm., height 0·29 mm., width 0·24 mm. Io. 2257, right valve, length 0·61 mm., height 0·27 mm.

REMARKS. *Paracypris terraefullonica* was originally described by Jones & Sherborn (1888 : 252) as *Macrocypris terrae-fullonicae*. Also described in the same publication is the ostracod *M. horatiana* which occupies a position within the publication previous to that of *M. terrae-fullonicae*. Both these species are considered to be synonymous. The decision to select *M. terrae-fullonicae* as the type was influenced by the better preservation of the specimen available and the preference in name, indicating as it does, derivation from the Bathonian Fullers-Earth.

Paracypris terraefullonica is similar to *Paracypris*? sp. *A*. Schmidt (1955 : 52) but differs posteriorly. In *P*.? sp. *A*. the posterior margin is close to the posterior cardinal angle, whilst that part of the valve behind the cardinal angle is more elongate. *P. bajociana* Bate (1963 : 186, pl. 2, figs. 1–8) has a much longer and more straight dorsal margin.

Superfamily **DARWINULACEA** Brady & Norman 1889

Family **DARWINULIDAE** Brady & Norman 1889

Genus ***DARWINULA*** Brady & Robertson 1885

REMARKS. *Darwinula stevensoni*, the type species, has the right valve larger than the left, a feature given as characteristic of the genus in the Treatise on Invertebrate Paleontology (Moore 1961 : 254). Several species of *Darwinula* are known, however, to possess a carapace in which the left valve is the larger. For example, the Recent *D. daps* Harding (1962 : 60, figs. 45–53) and the Purbeckian *D. leguminella* (Forbes *in* Lyell 1855 : 294, text-fig. 334*c*). Many more species are so described in the literature. *D. incurva* sp. nov., described below also possesses a carapace in which the left valve is the larger.

Darwinula incurva sp. nov.

(Pl. 1, figs. 7–12)

1965 *Darwinula* sp.A. Bate : 751, pl. 109, figs. 1–4.

DIAGNOSIS. *Darwinula* of large size with broadly arched dorsum, rounded anterior and posterior, and strongly incurved ventral margin anterior of valve centre. Left valve strongly overlaping right along ventral margin and around posterior. Anteriorly left valve over-reaching right. Shell surface finely punctate. Muscle scars as for family.

HOLOTYPE. Io.2259, a complete carapace from bed Q Kings Cliffe.

PARATYPES. Io.2260–74, from bed Q Kings Cliffe, and beds O & R Ancaster.

DESCRIPTION. **Carapace** oval-elongate, very finely punctate, appearing smooth in most specimens, although the internal surface of the valves is quite strongly punctate. Greatest length passes either through or just below mid-point, being dependent upon the outline of the anterior margin which may be either broadly rounded or extended forward slightly below mid-length. Posterior broadly rounded with the greatest width situated in the posterior third. Greatest height median. Dorsal margin arched. Ventral margin convex in the posterior half, strongly and characteristically incurved antero-medially. Left valve larger than the right which it strongly overlaps around the posterior and along the ventral margin. Around the anterior the overlap is replaced by overreach though along the antero-and postero-dorsal slopes overlap of the right valve by the left is noticeable. **Muscle scars** typical of the genus, consisting of a rosette of scars which in one specimen is composed of eleven in number. **Inner margin** and **line of concrescence** coincide anteriorly (not seen posteriorly) where a narrow **duplicature** is present. The surface of the duplicature in the left valve is serrated at right angles to the inner margin. The purpose of this is conjecture at the moment. Anterior **radial pore canals** short, straight and evenly spaced, about 20 in number. A long, narrow groove extends along the dorsal margin of the right valve, into which the dorsal margin of the left valve fits for purposes of articulation.

DIMENSIONS. Holotype. Io.2259, carapace, length 1·03 mm.; height 0·43 mm.; width 0·37 mm.

Paratypes. Io.2260, carapace, length 1·03 mm.; height 0·48 mm.; width 0·40 mm. Io.2261, left valve, length 0·83 mm.; height 0·37 mm.

REMARKS. *Darwinula* sp. *A*. Bate 1965 is a juvenile instar of the present species and is here placed into synonymy. Comparison with other British Mesozoic darwinulids shows *D. incurva* to be larger, more elongate and more strongly incurved than previously described species. *D. incurva* is similar in outline to *D. tubiformis* Ljubimova (1956 : 119, pl. 23, figs. 1*a*–*b*.) from the Lower Cretaceous of Mongolia but differs in not being so strongly swollen posteriorly and in being more slender in dorsal view. *D. barabinskensis* Mandelstam (as figured in Ljubimova 1960 : 28, pl. 2, fig. 2) from the Lower Cretaceous of the western Siberian Lowlands (Krasnoyarsk region) is close to *D. incurva* in dorsal outline but does not taper quite so much anteriorly neither is it as incurved antero-ventrally.

Superfamily **CYTHERACEA** Baird 1850

Family **LIMNOCYTHERIDAE** Klie 1938

Subfamily **TIMIRIASEVIINAE** Mandelstam 1960

Genus ***BISULCOCYPRIS*** Pinto & Sanguinetti 1958

REMARKS. As stated elsewhere (Bate 1965) difference of opinion exists relating to the validity of the two genera *Bisulcocypris* and *Theriosynoecum*. Sylvester-Bradley & Pinto (MS.) are currently of the opinion that within the Timiriaseviinae there are two distinct genera, one with hollow tubercles (*Theriosynoecum*), the other with or without solid tubercles (*Bisulcocypris*). An opinion with which I am in full agreement.

The presence of tubercles amongst these fresh to brackish water ostracods would appear to be either a genotypic or a phenotypic character. In those species which are normally without such ornamentation but which occasionally show it—it is conceivable that the presence of tubercles is in some way controlled by the environment (pH, salinity etc.) and as such would be a phenotypic character. There appears to be a definite division between those species which show this possible phenotypic variation and those in which the tubercles are genotypically controlled. The genus *Theriosynoecum* is considered to fall into the latter category, whilst in *Bisulcocypris* both phenotypic and genotypic tuberculate species occur. A genotypic species is one in which tubercles are present through all the ontogenetic stages, whilst a phenotypic species only shows the development of tubercles or nodes in the adult stage, and then, as appears to be often the case, in only one dimorph. In *B. anglica* sp. nov., for example, the nodes are characteristically developed in the male dimorph only.

Bisulcocypris anglica sp. nov.

(Pl. 2, figs. 1–11)

1965 *Bisulcocypris* sp. *A.*, Bate : 753, pl. 109, figs. 13, 14.

DIAGNOSIS. *Bisulcocypris*, oval/elongate in side view, tapering slightly to anterior. Posterior tapered in female dimorph. Greatest height at posterior cardinal angle. Ventro-lateral margin strongly convex, overhanging ventral surface. Two, short, crescentic sulci extend down from dorsal margin in anterior half of valve. Shell surface laterally punctate to reticulate. Ventro-lateral and ventral surfaces with strong lateral ridges. Slender males may possess small nodes in posterior half; females without nodes. Female with characteristic narrow posterior, produced by steeply sloping posterodorsal margin of posterior swelling. Male tending to have broader (height) posterior. Hinge lophodont. Valves equivalve.

HOLOTYPE. Io.2275, female carapace from bed Q, Kings Cliffe.

PARATYPES. Io.2276–99. Locality as above.

DESCRIPTION. **Carapace** oval/elongate with the greatest height being in the posterior half at the posterior cardinal angle in adults but is situated at the anterior cardinal angle in juveniles. Greatest length through or slightly below mid-point. Greatest width in the posterior half in female dimorphs, median in the male. Posterior broadly rounded in the male dimorph whilst in the posteriorly swollen female the posterior becomes much narrower (height) due to the steeply sloping dorsal surface of the posterior swelling. Posterior cardinal angle sharply angled in both sexes, anterior cardinal angle shallow, broadly rounded sweeping down to the narrowing anterior margin. Dorsal margin medially concave in the female dimorph, but less noticeably so in the male. Ventro-lateral margin strongly convex, overhanging the ventral surface. Shell surface strongly punctate to reticulate. Prominent lateral ridges extend along the ventro-lateral and ventral surfaces. In the male dimorph a number of small nodes (usually two in number) may occur in the posterior half of the carapace. One node is positioned just below and behind valve centre with the second node a short distance below and in front of this. In a single male, two smaller nodes occur dorsal to these. Two very small nodes are situated at the extreme posterior and a number around the anterior margin of both sexes. These are the only ones which occur in the female. Occasionally the median node described for the male is found also in a juvenile instar. Juveniles tend to be rather square in outline. Two, shallow, rather concentric sulci extend for a short distance only from the dorsal margin. Both sulci are situated in the anterior half of the carapace. Both left and right valves are of equal size. Along the ventral margin there is no overlap; postero-ventrally the right valve over-reaches the left whilst at the position of the antero-median incurvature the left over-reaches the right. Along the antero-dorsal slope the left valve progressively over-reaches the right with the maximum over-reach being at the anterior cardinal angle. Behind this angle the right valve strongly over-reaches the left for a short distance. Very slight overlap of the right by the left occurs at the posterior cardinal angle. **Muscle scars** are situated low down on the lateral part of the carapace below the first more medially situated sulcus, and consist of a backwardly sloping row of four adductor scars. Muscle scars anterior to these have not been observed. **Hinge** lophodont, only observed in the right valve where the median groove is long and rather broad. The anterior tooth is large and blade-like, being an enlarged, flattened continuation of the **selvage**. Posterior tooth not seen. From the dorsal view of a complete carapace it is obvious that an accommodation groove is present in the posterior half of the left valve. Around the anterior the **inner margin** and **line of concrescence** do not quite coincide. The separation is not really sufficient, however, for a **vestibule** to be developed. Anterior **radial pore canals** long and straight extending into the broad anterior **flange**, approximately 20 in number.

Dimensions. Holotype. Io.2275, female carapace, length 1·00 mm.; height 0·58 mm.; width 0·58 mm.

Paratypes. Io.2277, male carapace, length 1·04 mm.; height 0·63 mm.; width 0·51 mm. Io.2278, male carapace, length 0·98 mm.; height 0·56 mm.; width 0·47 mm. Io.2279, female carapace, length (broken) 0·98 mm.; height 0·66 mm.; width 0·68 mm. Io.2280, juvenile carapace, length 0·61 mm.; height 0·35 mm.; width 0·28 mm.

Remarks. The development of nodes in this species is restricted in adults to the male dimorphs and to a number of juvenile instars. Possibly those juveniles which show this feature may have been immature males, although there is no way of confirming this. *Bisulcocypris anglica* is close to *B. tenuimarginata* (Oertli 1957 : 765, pl. 23, figs. 15–24), specimens of which were kindly sent to me by Dr. Oertli, but is a much larger more elongate species. The anterior half of *B.*

tenuimarginata is quite short and stubby when compared with the elongate anterior of *B. anglica*. The French species does not appear to show any tendency towards the development of lateral nodes. *Bisulcocypris* sp. *A*. described from the Bathonian of Oxfordshire is considered to belong to this species.

Bisulcocypris ancasterensis sp. nov.

(Pl. 3, figs. 1–10)

1965 *Bisulcocypris* sp. *B* ; Bate : 753, pl. 109, figs. 10–12.

DIAGNOSIS. *Bisulcocypris* rectangular in outline with height at anterior cardinal angle almost equal to that at posterior cardinal angle. Strongly bi-sulcate, dimorphic. Shell surface punctate/reticulate with three nodes in posterior half and two nodes in anterior half. Smaller additional nodes occur at extreme posterior and anterior. Both nodes and surface ornamentation more positively developed in juvenile instars. Muscle scars as for genus.

HOLOTYPE. Io.2282, female carapace from bed R, Ancaster.

PARATYPES. Io.2283–5, 2300–1, from bed R, Ancaster.

DESCRIPTION. **Carapace** rectangular, dimorphic, rounded anteriorly and posteriorly. Dorsal and ventral margins in the male dimorph are almost parallel with only a shallow concavity medially. In the female, identified by the swollen posterior half, the dorsal margin is quite strongly concave medially. Ventro-lateral margin in both dimorphs overhangs the ventral surface as viewed laterally. Greatest length through mid-point with greatest height and width in posterior half in males and females; greatest height in anterior half in juveniles. Carapace in the anterior half bi-sulcate, the posterior sulcus being the better developed of the two; this is especially true in the female dimorph. The adductor **muscle scars** which consist of an oblique row of four scars, are situated at the base of this sulcus. Cardinal angles distinct. Shell surface punctate to reticulate, further ornamented by a number of prominent nodes. In the posterior half of the carapace three nodes are arranged in a triangular pattern; a large central node with one of equal size situated in front and below this and a smaller node situated behind and below. Smaller nodes may occur above these and on the posterior. In the anterior half two nodes are present; one in front of the ventro-lateral termination of the posterior sulcus and the second, much higher up, in front of the termination of the anterior sulcus. Ventral surface ornamented with low, longitudinal ridges. Left valve larger than the right, which it overlaps along the ventral margin, especially mid-ventrally, and again at the anterior and posterior cardinal angles. There is no terminal overlap. Mid-dorsally the right valve over-reaches the left. Juvenile instars reticulate with well developed nodes. Posteriorly the two low nodes which occur dorsally above the main group of three in the adults are here strongly developed and are equal in dominance to the others. Internal details have not been observed in the present material but have been described for *B.* sp. *B.* (see Bate; 1965 : 754).

DIMENSIONS. Holotype. Io.2282, female carapace, length 0·91 mm.; height 0·55 mm.; width 0·51 mm.

Paratypes. Io.2284, male carapace, length 0·98 mm.; height 0·51 mm.; width 0·36 mm. Io.2285, juvenile carapace, length 0·61 mm.; height 0·35 mm.; width 0·21 mm.

REMARKS. *Bisulcocypris ancasterensis* sp. nov., in being strongly nodose differs at once from *B. anglica* sp. nov., and *B. tenuimarginata* (Oertli). Moreover, it may also be distinguished from the above in outline (having a much deeper anterior than found in *B. anglica* and a much more elongate anterior half than that occurring in *B. tenuimarginata*) and by the more strongly developed second sulcus, never developed to such an extent in the other two species. *Bisulcocypris* sp. *B.* described from the Bathonian of Oxfordshire is almost certainly conspecific with the present species, despite its larger size.

Family **BYTHOCYTHERIDAE** Sars 1926

Genus ***MONOCERATINA*** Roth 1928

Monoceratina scarboroughensis Bate

(Pl. 3, fig. 11)

1965 *Monoceratina scarboroughensis* Bate : 99, pl. 1, figs. 1–12.

REMARKS. A single female carapace, of good preservation has been found in bed B in the Kettering section. The range of this species is thus extended from the Bajocian (*blagdeni* in part) into the Bathonian, although here again correlation of the horizons with known ammonite zones has not been possible.

Family **CYTHERIDEIDAE** Sars 1925

Subfamily **CYTHERIDEINAE** Sars 1925

Genus ***FABANELLA*** Martin 1961

REMARKS. Although placed by Martin into the Cytheridae, *Fabanella* is here considered to be more closely allied to the Cytherideidae on account of the shape and structure of the carapace, simple pore canals and muscle scar pattern. Although the antennal scar is not so strongly U-shaped as for the nominal genus Martin's illustration (pl. 1, fig. 5*b*) for the type species indicates that the arrangement is the same and belongs to Type **B** (Bate 1963 : 181, figs. 8–10).

Fabanella bathonica (Oertli)

(Pl. 4, figs. 1–5)

1957 *Cyprideis*? *bathonica* Oertli : 758, pl. 21, figs. 12–20, pl. 22, figs. 1–6, 11, 12, (*Non*. figs. 7, 8, ? figs. 9, 10).
1963 *Fabanella bathonica* (Oertli) Oertli, pl. 28 (2), fig. *m*.

MATERIAL. Specimens registered in the collections: Io.2303–15 from bed R, Kings Cliffe and bed U, Ancaster.

REMARKS. *Fabanella bathonica* does not occur generally throughout the Upper Estuarine Series, being restricted to only a few horizons. However, when it does occur it is a common species amongst a marine to brackish-water fauna. Specimens of this species were kindly sent to me for comparison purposes by Dr. Oertli.

Subfamily **GALLIAECYTHERIDEINAE** Andreev & Mandelstam 1964

REMARKS. The subfamily Galliaecytherideinae introduced by Andreev & Mandelstam contains genera which although possessing some external resemblance to those placed in the Schulerideidae are nevertheless distinguished by their possession of a type **A** muscle scar pattern and simple radial pore canals. The genus *Galliaecytheidea* Oertli (1957 : 654) was placed into the Schulerideidae in error by Bate (1963 : 207), a situation which is here corrected.

Andreev & Mandelstam include within their new subfamily the following genera: *Galliaecytheridea* Oertli, *Lyubimovina* Neale, *Palaeocytheridella* Mandelstam, *Asciocythere* Swain, *Rubracea* Mandelstam and *Procytheridea* Peterson. In the present paper, however, *Asciocythere, Procytheridea* and *Rubracea* are not considered to belong here. *Belekocytheridea* gen.nov. and *Pichottia* Oertli are considered to belong to this subfamily. Van Morkhoven (1963 : 307) considers the genus *Palaeocytheridella* Mandelstam to be a junior synonym of *Vernoniella* Oertli.

Subfamily **GALLIAECYTHERIDEINAE** Andreev & Mandelstam 1964

Genus ***GALLIAECYTHERIDEA*** Oertli 1957

Galliaecytheridea? ***kingscliffensis*** sp. nov.

(Pl. 4, figs. 6–12; Pl. 5, figs. 1–8)

DIAGNOSIS. *Galliaecytheridea*?, dimorphic: females plump, subquadrate with backwardly sloping dorsal margin and concave postero-dorsal margin, producing short, upturned posterior. Males elongate. Both sexes with compressed anterior marginal border. Shell surface very finely punctate. Hinge entomodont. Muscle scars type **A**. Radial pore canals, straight, widely spaced; 9 anteriorly; 4 posteriorly.

HOLOTYPE. Io.2316, female carapace, bed S, Kings Cliffe.

PARATYPES. Io.2317–27, beds J & S, Kings Cliffe and bed W, Ancaster.

DESCRIPTION. **Carapace** plump and subquadrate in outline with triangular-shaped posterior, slightly upturned, in the female dimorph. Males more elongate in outline but otherwise similar. Greatest length of the carapace passes through mid-point and the greatest height in the anterior half; through the anterior cardinal angle in the female but just behind this in the male. Greatest width median. In dorsal view the carapace is noticeably convex, especially in the female, with compressed anterior and posterior marginal borders. Dorsal margin straight or very slightly convex, sloping to the posterior, again more noticeably so in the female. Cardinal angles prominent. Anterior broadly rounded; posterior broadly triangular with a concave postero-dorsal slope producing a slight upturning. Ventral margin medially incurved, obscured in a whole carapace by the median convexity of the ventro-lateral margin. Shell surface very finely punctate with small, widely scattered, circular **normal pore canal** openings. There is no definite **eye swelling**, although a short, diagonal furrow, as found in such genera as *Praeschuleridea* and *Schuleridea*, occurs below the anterior cardinal angle. Here, however the groove may be seen in both valves. In the previously mentioned genera it is generally a feature of the right valve only. Left valve larger than the right which it overlaps along the ventral margin and over-reaches along the antero-, and postero-dorsal and dorsal margins. Terminally there is neither overlap nor over-reach. **Hinge** entomodont: left valve with terminal, elongate, loculate sockets separated by a strong median bar which is dentate along its length. The denticles of the median bar are very much enlarged in the anterior section. Above the median element a broad, deep, accommodation groove is developed. In the right valve there are six posterior teeth and probably a similar number anteriorly although damaged in the present material. The median groove which is loculate is expanded considerably in its anterior section. **Muscle scars** consist of a vertical row of four oval adductor scars with a single, round antero-dorsal antennal scar which is situated opposite the top two adductor scars. Mandibular scar crescent-shaped and antero-ventral in position. This muscle scar pattern thus falls into type **A**. **Inner margin** and **line of concrescence** coincide, producing a **duplicature** of moderate width. **Radial pore canals** straight and widely spaced, nine anteriorly and approximately four posteriorly. In single valves, the incurved part of the ventral margin can be seen to be obscured ventrally by a flattened " lip " convex downwards.

DIMENSIONS. Holotype. Io.2316, female carapace, length 0·62 mm.; height 0·45 mm.; width 0·36 mm.

Paratypes. Io.2317, female carapace, length 0·64 mm.; height 0·44 mm.; width 0·35 mm. Io.2318, male carapace, length 0·71 mm.; height 0·43 mm.; width 0·35 mm. Io.2321, female left valve, length 0·64 mm.; height 0·45 mm. Io.2322, male left valve, length 0·69 mm.; height 0·43 mm. Io.2326, female right valve, length 0·58 mm.; height 0·36 mm.

REMARKS. *Galliaecytheridea*? *kingscliffensis* sp. nov. is placed into the genus with a query owing to the fact that the hinge, in being entomodont, is quite unlike that found in any other species of this genus. It is not proposed to erect a subgenus to contain this species at this stage. The dimorphism found here is more clearly apparent than in other members of the genus. In fact the male dimorphs bear some resemblance to *Galliaecytheridea postrotunda* Oertli (1957 : 656, pl. 2, figs. 45–55) although they do not taper so noticeably towards the posterior nor do they possess a posterior spine. The female dimorphs on the other hand are close to *G. dissimilis* Oertli (1957 : 655, pl. 1, figs. 32–49, pl. 2, figs. 40–44) from which they may be distinguished by their greater convexity (in dorsal view), dorsal margin with a slightly more pronounced slope to the posterior and by the presence of an entomodont hinge.

Genus ***BELEKOCYTHERIDEA*** nov.

Type species. *Belekocytheridea punctata* sp. nov.

Diagnosis. Galliaecytherideinae with bean-shaped carapace; straight, somewhat flattened dorsal margin; antero-ventral and postero-ventral margins characteristically convex, projecting slightly below line of ventral surface. Antero-dorsal slope short, passing into uniformly rounded anterior. Postero-dorsal slope long, slightly convex. Cardinal angles prominent. Posterior narrowly rounded with greatest length passing below mid-point. Left valve larger than right. Hinge antimerodont; accommodation groove poorly developed. Inner margin and line of concrescence coincide. Radial pore canals straight, widely spaced, approximately 9 anteriorly and 5 posteriorly. Muscle scars a vertical row of 4 oval adductors with antero-dorsal antennal scar and antero-ventral mandibular scar (Type **A**).

Remarks. The genus *Belekocytheridea* may be distinguished from all other ostracods by its characteristic, rather angular bean shaped carapace. At the present time only the type species has been definitely placed into the genus although a small number of specimens of a much larger species have been found within the Bajocian Upper Lincolnshire Limestone. These will be considered in a separate publication. The ecology of the type species suggests that the genus may be marine to brackish water in habit. In this it resembles *Lycopterocypris* Mandelstam 1956, a genus having a similar external appearance but internally distinguished by the presence of an Adont hinge.

Belekocytheridea punctata sp. nov.

(Pl. 5, figs. 9–13, Pl. 6, figs. 1–5)

Diagnosis. *Belekocytheridea* with ventral and ventro-lateral surfaces ornamented by fine, longitudinal striae which terminally pass up onto lateral surface of carapace to parallel anterior and posterior margins. Terminally striae poorly developed, dying out before reaching dorsal margin. Remainder of lateral surface punctate. Species dimorphic. Hinge and muscle scars as for genus.

Holotype. Io.2328, female carapace, bed H, Ketton.

Paratypes. Io.2329–57, male and female carapaces and single valves, bed H, Ketton; bed R, Ancaster and bed G, Kings Cliffe.

Description. **Carapace** bean shaped, convex in dorsal view, with prominent cardinal angles when viewed laterally. Dorsal margin straight, very slightly convex. Antero-dorsal slope short passing into rounded anterior margin. Postero-dorsal slope long, slightly convex and passing into narrowly rounded posterior. Ventral margin incurved medially, overhung laterally by the convex ventro-lateral margin. Terminally the convex antero-ventral and postero-ventral margins project slightly below the ventral surface. Sexual dimorphism strongly apparent, the presumed males being very much more elongate but otherwise morphologically similar to the shorter female dimorphs. Greatest length of carapace occurs below mid-point whilst greatest height occurs at the posterior cardinal angle and greatest width through mid-point. Shell surface punctate laterally; terminally with weak striae paralleling the margins, the striae extending on to the lateral surface from the ventral surface. **Normal pore canal** openings circular, prominently developed and well spaced over the lateral surface. Left valve larger than the right which it overlaps along the ventral margin and strongly along the antero-, and postero-dorsal slopes. Terminally and dorsally there is no overlap. **Hinge** antimerodont; left valve with elongate terminal loculate sockets and a denticulate median bar. Accommodation groove virtually absent. Right valve with approximately 5–6 terminal teeth and an elongate locellate median bar. **Inner margin** and **line of concrescence** coincide, **duplicature** being of moderate width. A narrow **flange** extends around the anterior margin. **Radial pore canals** long and straight, widely spaced; 9 anteriorly and 5 posteriorly. **Muscle scars** (Type A) with the 4 adductors in a vertical row, the large rounded antennal scar being antero-dorsal in position. Mandibular scar antero-ventral.

DIMENSIONS. Holotype. Io. 2328, female carapace, length 0·57 mm.; height 0·31 mm.; width 0·29 mm.

Paratypes. Io. 2329, male carapace, length 0·66 mm.; height 0·33 mm.; width 0·29 mm. Io. 2331, female carapace, length 0·54 mm.; height 0·30 mm.; width 0·27 mm. Io. 2356, male left valve, length 0·68 mm.; height 0·38 mm.

REMARKS. *Belekocytheridea punctata* sp. nov., is quite unlike any previously described species and has, therefore, been placed into a new genus. The specimens, already referred to, as occurring in the Upper Lincolnshire Limestone are quite smooth whilst the present species has a partial ornamentation of longitudinal striae.

Genus ***PICHOTTIA*** Oertli 1959

REMARKS. In the original diagnosis of *Pichottia* by Oertli (1959 : 115), size was considered to be a diagnostic character. This was based upon the very small size of the type species where the length of the female was in the order of 0·37–0·41 mm.; and that of the male 0·43–0·47 mm. In *Pichottia magnamuris* sp. nov., described below, the length of the female dimorph is in the region of 0·61–0·69 mm.; and that of the male 0·68–0·76 mm. A small size should not, therefore, be considered to be diagnostic of this genus.

Pichottia magnamuris sp. nov.

(Pl. 6, figs. 6–14, Pl. 7, figs. 1–6)

DIAGNOSIS. *Pichottia*, plump, strongly convex in dorsal view, oval in lateral view. Dimorphic. Shell surface very finely punctate. Females of length 0·61–0·69 mm.; males of length 0·68–0·76 mm.

HOLOTYPE. Io.2358, female carapace, bed S, Kings Cliffe.

PARATYPES. Io.2359–68, male and female carapaces and single valves from bed S, Kings Cliffe and Dane Hill.

DESCRIPTION. **Carapace** plump, strongly convex in dorsal view, the valves parting slightly at extreme anterior. Ovoid in lateral view tapering to the narrowly rounded posterior. Male dimorphs more elongate than the females, more strongly tapering posteriorly and not so convex in dorsal view. Anterior rounded with long, convex antero-dorsal slope; short convex dorsal margin and long postero-dorsal slope, strongly convex in the female, long and steeply sloping in the male. Posterior narrowly rounded. Ventro-lateral margin convex, overhanging the ventral surface in side view. Ventral margin antero-medially incurved. Cardinal angles broadly rounded. Greatest length of carapace passes below mid-point. The position of greatest height occurs at the posterior cardinal angle although the height at the anterior cardinal angle is only very slightly less. Greatest width behind mid-point. Left valve slightly larger than the right, which it overlaps along the ventral margin, and along the antero-dorsal and postero-dorsal slopes. Shell surface punctate with small, round, **normal pore canal** openings evenly but widely spaced over the carapace. **Hinge** antimerodont: left valve with elongate, strongly loculate terminal sockets, separated by a very short but strongly dentate median bar, above which there is a small accommodation groove. Right valve with 6–7 terminal teeth and a short, loculate median groove. **Inner margin** and **line of concrescence** coincide, **duplicature** of moderate width. **Radial pore canals** short, straight and few in number; 5 posteriorly, up to 13 anteriorly. **Muscle scars** of type **A** (Bate, 1963 : 180). Four oval adductor scars are situated in a vertical row with a large antennal scar situated in front of the uppermost two adductor scars. A much smaller mandibular scar is situated antero-ventrally to the adductors.

DIMENSIONS. Holotype. Io.2358, female carapace, length 0·62 mm.; height 0·37 mm.; width 0·37 mm.

Paratypes. Io.2360, male carapace, length 0·68 mm.; height 0·37 mm.; width 0·34 mm. Io.2362, female left valve, length 0·60 mm.; height 0·36 mm. Io.2363, female right valve, length 0·65 mm.; height 0·37 mm. Io.2366, male left valve, length 0·75 mm.; height 0·41 mm. Io.2367, male right valve, length 0·76 mm.; height 0·38 mm.

REMARKS. *Pichottia magnamuris* sp. nov. is very close to *P. muris* Oertli (1959 : 116, pl. 1, figs. 1–10), specimens of which were kindly sent to me by Dr. Oertli, but differs in being very much larger, generally not so acuminate posteriorly and in being more noticeably convex dorsally and ventro-laterally.

Family **SCHULERIDEIDAE** Mandelstam 1959

Subfamily **SCHULERIDEINAE** Mandelstam 1959

Genus ***SCHULERIDEA*** Swartz & Swain 1946

EMENDED DIAGNOSIS. Carapace subovoid with greatest length subventral. Dorsal margin convex, umbonate in larger left valve. Posterior narrowly rounded. Eye swelling either restricted to right valve or present as prominent node on both valves. Hinge paleomerodont. Muscle scars, type **C**. Anterior radial pore canals splayed fan-like, varying in number from 10 to approximately 100. Inner margin and line of concrescence coincide. Shell surface without strong ornamentation.

REMARKS. The genus *Schuleridea* was erected by Swartz & Swain (1946) with the type species being described from the Upper Jurassic, Schuler formation, Louisiana. In the following year (1947) Mandelstam erected the genus *Aequacytheridea* with the Tertiary ostracod, *Cytheridea perforata* (Roemer) as type. Both *Aequacytheridea* and *Schuleridea* possess a paleomerodont hinge, type **C** muscle scar pattern (Bate 1963 : 181) and anterior radial pore canals arranged fan-like and curving outwards away from a line drawn through mid-point. Subsequently (Chernysheva 1960 : 370 and Moore 1961 : Q 284) these two genera were considered to be synonymous, *Aequacytheridea* being the junior synonym.

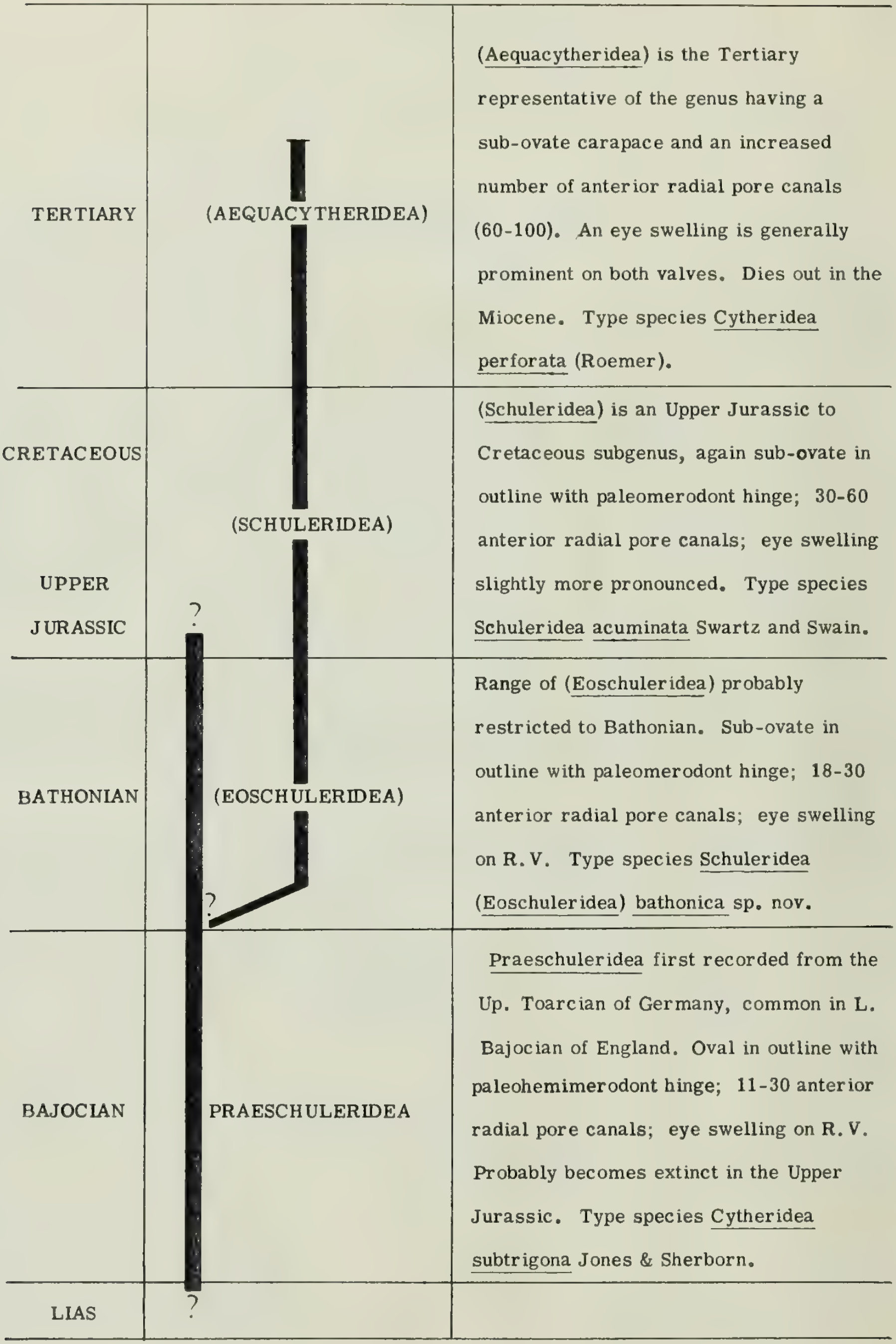
Malz (1958 : 120) noted the evolutionary increase in the number of radial pore canals and considered *Aequacytheridea* to be a subgenus of *Schuleridea*. Kollmann (1960 : 185) recognized 3 subgenera for *Schuleridea*: *Schuleridea* (*Schuleridea*) Swartz & Swain 1946, *Schuleridea* (*Aequacytheridea*) Mandelstam 1947 and *Schuleridea* (n. subgen?)

The three subgenera were not diagnosed nor was the third subgenus named.

The Bathonian species of *Schuleridea* described in the present paper possesses some 18–20 anterior radial pore canals, a number much lower than for previously described species. The number of anterior radial pore canals is considered here to indicate sub-generic identification. Accordingly three subgenera are here recognized: *Schuleridea*, *Aequacytheridea* and a new subgenus, *Eoschuleridea*. All three form an evolutionary sequence with *Eoschuleridea* probably evolving from the genus *Praeschuleridea* Bate (1963 : 207) in early Bathonian or late Bajocian times.

The broad stratigraphic position of the three subgenera and the evolution from *Praeschuleridea* is shown in Table I below. For convenience a numerical range of anterior radial pore canals is given for each subgenus. Overlap at the boundaries is to be expected in any continuous sequence.

The increase in number of the anterior radial pore canals is shown in Table I to be without any break between the three subgenera. This is, at the moment, a purely artificial grouping with each of the subgenera concerned tending to fall somewhere about the centre of the number of pore canals suggested. When the majority of the species for all the subgenera have been described, a more exact range in the number of anterior pore canals may be possible.



TERTIARY	(AEQUACYTHERIDEA)	(Aequacytheridea) is the Tertiary representative of the genus having a sub-ovate carapace and an increased number of anterior radial pore canals (60-100). An eye swelling is generally prominent on both valves. Dies out in the Miocene. Type species Cytheridea perforata (Roemer).
CRETACEOUS UPPER JURASSIC	(SCHULERIDEA) ?	(Schuleridea) is an Upper Jurassic to Cretaceous subgenus, again sub-ovate in outline with paleomerodont hinge; 30-60 anterior radial pore canals; eye swelling slightly more pronounced. Type species Schuleridea acuminata Swartz and Swain.
BATHONIAN	(EOSCHULERIDEA) ?	Range of (Eoschuleridea) probably restricted to Bathonian. Sub-ovate in outline with paleomerodont hinge; 18-30 anterior radial pore canals; eye swelling on R.V. Type species Schuleridea (Eoschuleridea) bathonica sp. nov.
BAJOCIAN	PRAESCHULERIDEA	Praeschuleridea first recorded from the Up. Toarcian of Germany, common in L. Bajocian of England. Oval in outline with paleohemimerodont hinge; 11-30 anterior radial pore canals; eye swelling on R.V. Probably becomes extinct in the Upper Jurassic. Type species Cytheridea subtrigona Jones & Sherborn.
LIAS	?	

TABLE I. *Evolutionary Series of* Praeschuleridea *and* Schuleridea.

It is interesting to note that just as the number of anterior radial pore canals increases throughout the evolution of the genus *Schuleridea* so also is it the case for *Praeschuleridea* which in the Bajocian (and Aalenian) never appears to possess more than 16 anterior radial pore canals, whereas within the Bathonian the number may be as high as 30.

Subgenus ***EOSCHULERIDEA*** nov.

DIAGNOSIS. *Schuleridea* having reduced number (18–30) anterior radial pore canals. Eye swelling poorly developed. Other details as for genus.

TYPE SPECIES. *Schuleridea* (*Eoschuleridea*) *bathonica* sp. nov.

REMARKS. As previously mentioned, *Eoschuleridea* is both morphologically and geologically situated between *Schuleridea* s.s. and *Praeschuleridea* from which it was most probably derived. The gradual increase in the number of anterior radial pore canals and the development of an eye node produces the evolutionary series indicated above.

Schuleridea* (*Eoschuleridea*) *bathonica sp. nov.

(Pl. 7, figs. 7–13, Pl. 8, figs. 1–11)

DIAGNOSIS. *Eoschuleridea* sub-ovate in side view, posteriorly acuminate in female dimorph, oval elongate in male dimorph. Dorsal margin arched, left valve more strongly umbonate in male dimorph. Shell surface punctate with equally spaced normal pore canal openings. Eye swellings indistinct. Eighteen to twenty anterior radial pore canals, 9 posterior canals. Larger left valve overlaping right valve on all sides. Hinge and muscle scars as for genus. Duplicature broad.

HOLOTYPE. Io.2369, female carapace, bed S, Kings Cliffe.

PARATYPES. Io.2370–94, male and female valves and carapaces from beds F & S, Kings Cliffe and bed H, Ketton.

DESCRIPTION. **Carapace** sub-ovate in outline, acuminate posteriorly in the female dimorph where the line of greatest length passes below mid-point. In the more elongate, oval, male dimorph, greatest length passes through mid-point. Greatest height just behind anterior cardinal angle in both dimorphs. Greatest width median. Anterior broadly rounded in the female, whilst the posterior is more narrowly rounded. In the male, both anterior and posterior are equally rounded. Ventro-lateral margin medially convex, ventral margin antero-medially incurved. Dorsal margin convex, especially in the left valve and particularly in the male where the left valve is decidedly " umbonate ". Cardinal angles rounded with the anterior angle right valve male and the posterior angle right valve female being the most sharply defined. Postero-dorsal slopes in the female larger and more nearly straight than in the male. Larger left valve overlaps the smaller right valve on all sides. Shell surface smooth or punctate, depending upon preservation with well developed normal pore canal openings evenly scattered over the valve. **Hinge** paleomerodont.

Left valve with elongate strongly loculate terminal sockets, anteriorly with 6 grooves and posteriorly with 8. Median, connecting groove short, and very finely locellate. Accommodation groove shallow and rather poorly developed. Right valve with terminal elongate dentate ridges bearing 6 anterior and 8 posterior teeth connected by a short, very finely denticulate ridge. The median element in the male dimorph is longer than that present in the female, the number of terminal teeth, is, however, the same. **Inner margin** and **line of concrescence** coincide the **duplicature** being quite broad, especially in the postero-ventral region. **Radial pore canals** long and curved. Anteriorly there appears to be generally 19 in number though 18 and 20 have been observed, arranged fan-like. Posteriorly there are 9 canals, of which 8 are situated below a line through mid-point. **Muscle scars** of type **C**. The four oval adductor scars form a concentric row around the antero-median oval antennal scar. The mandibular scar is antero-ventral in position.

DIMENSIONS. Holotype. Io.2369, female carapace, length 0·74 mm.; height 0·43 mm.; width 0·36 mm.

Paratypes. Io.2370, male carapace, length 0·80 mm., height 0·47 mm., width 0·38 mm. Io.2373, female right valve, length 0·65 mm.; height 0·39 mm. Io.2375, female left valve, length 0·70 mm.; height 0·46 mm. Io.2376, female right valve, length 0·67 mm.; height 0·40 mm. Io.2378, male right valve, length 0·77 mm.; height 0·41 mm. Io.2379, male left valve, length 0·74 mm.; height 0·43 mm.

REMARKS. *Schuleridea* (*Eoschuleridea*) *bathonica* sp. nov., may be distinguished from described species of *Schuleridea* not only on variations in the outline but in the number of radial pore canals present. The male dimorph of this species, externally resembles the male dimorph of *Galliaecytheridea*? *kingscliffensis* but may be distinguished by its more oval outline, strongly umbonate left valve and internally by the hinge, muscle scars and radial pore canals.

Genus ***PRAESCHULERIDEA*** Bate 1963

Praeschuleridea quadrata sp. nov.

(Pl. 9, figs. 1–12)

DIAGNOSIS. *Praeschuleridea* with oval carapace in male dimorph, dorsally arched in female. Both dimorphs with distinctly angled posterior cardinal angle. Shell surface punctate. Hinge not strongly paleohemimerodont. Radial pore canals, varying from 20–30 anteriorly.

HOLOTYPE. Io.2395, female carapace, bed R, Kings Cliffe.

PARATYPES. Io.2396–2413, male and female valves and carapaces, beds R & S, Kings Cliffe.

DESCRIPTION. **Carapace** sub-trigonal in the female dimorph, arched dorsally, with greatest height passing through mid-point. In the male dimorph the carapace is oval-elongate with greatest height being just behind the anterior cardinal angle.

Characteristically in both dimorphs the posterior cardinal angle is sharply angled and in the female set high up away from the posterior. Dorsal margin long and gently convex in the male, umbonate and strongly convex in the female. Anterior cardinal angle in both cases, broadly rounded. Anterior and posterior broadly rounded in the male, posterior more narrowly rounded in the female. Ventral margin convex, incurved slightly antero-medially. Postero-dorsal slope longer in the female than in the male. Greatest length through mid-point in the male, slightly below this in the female. Greatest width median in both dimorphs. Shell surface punctate with rather large, circular **normal pore canal** openings. Left valve larger than the right which it overlaps on all sides other than dorsally, in which region the left valve over-reaches the right. **Hinge** paleohemimerodont. Left valve with terminal loculate sockets connected by a short locellate groove which extends over a low median bar. In male dimorphs the median groove is virtually impossible to distinguish, whilst it is extremely well developed in the female. In some material the dorsal edge of the groove projects noticeably above the groove. Above the median element there is an elongate/triangular accommodation groove. In the right valve the dentate terminal elements consist of anteriorly 6 teeth and posteriorly 7 teeth corresponding with the terminal sockets in the left valve. Median ridge low and rather poorly defined. **Inner margin** and **line of concrescence** coincide producing a **duplicature** of moderate width. Anterior **radial pore canals** splayed fan-like, curving outwards from a line drawn through mid-point. The number present varies within individuals from 20–30. Posteriorly the pore canals also curving away from a line drawn through mid-point are situated largely below this line and vary from approximately 9–18. **Muscle scars**, type **C**: Adductor scars form a slightly crescentic row in front of which is an oval antennal scar, the long axis of which is vertical.

DIMENSIONS. Holotype. Io.2395, female carapace, length 0·63 mm.; height 0·43 mm.; width 0·34 mm.

Paratypes. Io.2397, male carapace, length 0·82 mm., height 0·48 mm.; width 0·37 mm. Io.2398, female left valve, length 0·64 mm.; height 0·45 mm. Io.2399, female right valve, length 0·56 mm.; height 0·35 mm. Io.2400, male left valve length 0·78 mm.; height 0·46 mm.

REMARKS. The hinge present in *Praeschuleridea quadrata* sp. nov., although paleohemimerodont, does not possess such a positive median element in the left valve as occurs in all the previously described species of the genus. A second feature of this species is that the number of radial pore canals has increased and appears to vary within the population. It is interesting to note also that those specimens which possess the larger number of anterior pore canals also possess the larger number of posterior canals.

The posterior cardinal angle in the present species is situated much higher up on the carapace than is the case in *P. subtrigona* (Jones & Sherborn), Bate (1963 : 207, pl. 12, figs. 12–16; pl. 13, figs. 1–9).

Schuleridea pentagonalis Swartz & Swain (1946 : 368, pl. 53, figs. 1–8) is externally similar to *Praeschuleridea quadrata* but may be distinguished by the outline of the dorsal margin which is strongly umbonate in the left valve of *P. quadrata* but only broadly convex in *S. pentagonalis*. Internal details for the latter are not known.

Family **CYTHERURIDAE** Müller 1894

Genus ***METACYTHEROPTERON*** Oertli 1957

Metacytheropteron drupacea (Jones)

(Pl. 10, figs. 1–9)

1884 *Cythere drupacea* Jones : 772, pl. 34, fig. 30.
1957*a* *Metacytheropteron* sp. 50 Oertli : table 1.

DIAGNOSIS. *Metacytheropteron* with elongate/sub-ovate carapace. Greatest height at anterior cardinal angle, posterior acuminate. Dorsal margin broadly convex, especially in left valve. Shell surface strongly ornamented with triangular arrangement of longitudinal and obliquely transverse ridges.

HOLOTYPE. IN.43498, female carapace from Richmond boring at 1205 ft., figured Jones 1884, pl. 34, fig. 30.

OTHER MATERIAL. Io.2414–18, single valves (male and female dimorphs) from bed M, Ketton.

DESCRIPTION. **Carapace** sub-ovate tapering strongly to the posterior in the female dimorph, rather more elongate in the male. Dorsal margin arched in the left valve, medially convex in the right. Anterior broadly rounded; posterior acuminate, with convex postero-ventral slope and concave postero-dorsal slope (convex in the male dimorph). Ventro-lateral margin convex, particularly in the female. Ventral margin with median incurvature. Greatest length of carapace passes slightly below mid-point; greatest height at the anterior cardinal angle in the left valve, median in the right; greatest width median. Shell surface strongly ornamented with a triangular arrangement of longitudinal and obliquely transverse ridges. The dorsal apex of the triangle (equilateral) meets the dorsal margin above valve mid-point. The centre of the triangle breaks down into a reticulate ornamentation. Ventral surface with 4–5 longitudinal ridges. Numerous **normal pore canal** openings are clearly seen only on the ventral and ventro-lateral surfaces. An oval-elongate **eye swelling** is only really clearly seen in the male dimorph just below the anterior cardinal angle. The deep, oblique groove present behind the eye swelling is, however, well developed in both dimorphs. Left valve larger than the right which it overlaps along the ventral margin and along the antero-dorsal slope, and probably also along the postero-dorsal slope. Anteriorly the left valve appears to merely extend beyond the right. Elsewhere the valve relationships are not clearly seen in the present material. **Hinge** antimerodont. Left valve with elongate loculate sockets and a denticulate median bar, above which there is only a very poorly developed accommodation groove. Right valve with approximately 6 posterior teeth and 8 anterior teeth, median groove locellate. **Inner margin** and **line of concrescence** coincide, although perhaps not exactly so around the anterior.

Radial pore canals straight, rather strongly developed and widely spaced, 8 anteriorly at least 3 posteriorly but probably no more than 4. **Muscle scars** not observed.

DIMENSIONS. Holotype. IN.43498, female carapace, length 0·50 mm.; height 0·30 mm.; width 0·29 mm.

Other material. Io.2414, female left valve, length 0·54 mm.; height 0·33 mm. Io.2415, male left valve, length 0·67 mm.; height 0·35 mm. Io.2416, male right valve, length 0·60 mm.; height 0·30 mm. Io.2417, male right valve, length 0·61 mm.; height 0·30 mm.

REMARKS. The holotype is the only complete carapace available at the present time and this has suffered a certain amount of crushing in the postero-dorsal region.

Dr. H. J. Oertli kindly loaned me material of the type species, *Metacytheropteron elegans* Oertli (1957 : 664, pl. 4, figs. 116–124) to compare with the species described here. Although very close to *M. elegans*, *M. drupacea* may be distinguished by the more strongly arched dorsal margin in the left valve and is, therefore, not so narrow and elongate in lateral view. Ornamentally *M. drupacea* has the more definitely triangular arrangement of ridges without such a large central reticulate development.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948

Genus ***PROGONOCYTHERE*** Sylvester-Bradley 1948

Progonocythere levigata sp. nov.

(Pl. 10, figs. 10–14, Pl. 11, figs. 1–9)

DIAGNOSIS. *Progonocythere* with subquadrate/elongate punctate carapace over which large, circular, normal pore canal openings are evenly spaced. Dorsal outline of left valve, female dimorph, characteristically umbonate, anterior cardinal angle being set well back only just in front of valve centre. Small marginal denticles may occur anteriorly and posteriorly in right valve. Ventro-lateral margin broadly convex. Anterior and posterior borders compressed. Internal details as for genus.

HOLOTYPE. Io.2419, female left valve, bed H, Ketton.

PARATYPES. Io.2420–33, carapaces and single valve (both dimorphs), bed H, Ketton.

DESCRIPTION. **Carapace** subquadrate with high, arched dorsal outline in the female dimorph, elongate in the male. Anterior broadly rounded with, in two right valves, a small group of denticles situated at mid-height. Posterior narrowly rounded situated high on the male carapace; at mid-height in the female left valve, subventral in the female right valve where a small group of denticles may be found on the postero-ventral slope. The postero-dorsal slope in both female valves is very steeply angled. Dorsal margin broadly convex in the male, steeply angled in the female, especially within the left valve where the anterior cardinal angle is situated just anterior of valve middle, producing an umbonate outline. Ventro-lateral margin strongly convex. Ventral margin with antero-median incurvature. Greatest length above mid-point in the male left valve; through mid-point in the female left valve, below mid-point in the right. Male right valve damaged but greatest length probably passes through mid-point. Greatest height through the anterior cardinal angle in the female, median in the male. Greatest width median. Anterior and posterior marginal borders compressed. Shell surface finely punctate with prominent, evenly spaced, **normal pore canal** openings. Left valve larger than the right which it overlaps along the ventral margin and slightly along the antero-dorsal slope. Elsewhere the left valve over-reaches the right. **Hinge** entomodont. Left valve with strongly loculate terminal sockets and a dentate median bar, the anterior portion of which is even more strongly dentate. A long, narrow accommodation groove is present above the median element. Right valve with 7 posterior teeth and an indeterminate number of anterior teeth (probably 8–9), and a loculate median groove, the anterior part of which is greatly expanded. **Inner margin** and **line of concrescence** coincide; **duplicature** only of moderate width. **Radial pore canals** not distinguished. **Muscle scars** of type A. The 4 adductor scars are in a subvertical row with the round antennal scar situated opposite and close to the most dorsal scar in the male. In the female the antennal scar is slightly lower in position and occurs a good deal further away from the adductors.

DIMENSIONS. Holotype. Io.2419, female left valve, length 0·81 mm.; height 0·54 mm.

Paratypes. Io.2420, female right valve, length 0·82 mm.; height 0·49 mm. Io.2421, male left valve, length 0·85 mm.; height 0·50 mm. Io.2422, male right valve, length (broken) 0·93 mm.; height 0·51 mm. Io.2423, female carapace, length 0·71 mm.; height 0·46 mm.; width 0·35 mm.

REMARKS. *Progonocythere levigata* approaches *P. cristata* Bate (1963 : 191, pl. 4, figs. 5–15, pl. 5, figs. 1–6) in outline but does not develop the ventro-lateral overhang characteristic of the latter. The male dimorph of *P. levigata* also is a much more oval ostracod in side view. *Progonocythere stilla* Sylvester-Bradley (1948 : 190, pl. 12, figs. 1, 2, pl. 13, figs. 1, 2) is easily distinguishable by its more truncated posterior.

Progonocythere rugosa sp. nov.

(Pl. 11, figs. 10–14, Pl. 12, figs. 1–9, Pl. 13, fig. 2.)

DIAGNOSIS. *Progonocythere* with coarse ornamentation of pits, grooves and ridges aligned parallel to ventro-lateral and terminal margins. Carapace subdivided by deep median, vertical sulcus. Ventro-lateral margin extended keel-like below ventral surface. Internal details as for genus.

HOLOTYPE. Io.2434, female carapace, bed S, Kings Cliffe.

PARATYPES. Io.2435–52, both dimorphs, carapaces and single valves from beds R & S, Kings Cliffe, Dane Hill, and bed S, Ketton.

Description. **Carapace** subquadrate, more elongate, however, in the male dimorph. Ventro-lateral margin strongly overhangs the ventral surface and tapers to form a keel-like structure, particularly in the postero-ventral region. Greatest length of carapace tends to pass slightly above mid-point in both dimorphs, the narrowly rounded posterior being set high up on the carapace. Anterior broadly rounded. Dorsal margin with slight concavity behind anterior cardinal angle, through which the line of greatest height passes. This angle is set further back in the female left valve than in the male; a condition which to some extent also applies in the right valve. Antero-dorsal slope tends to be rather long and convex, whilst the postero-dorsal slope is concave and much shorter. Greatest width just behind the median sulcus. Anterior and posterior marginal borders compressed. Ventral margin distinctly incurved antero-medially. Shell surface strongly ornamented. Ventrally the V-shaped ventral surface, bounded on either side by the ventro-lateral overhang, is ornamented by 3 prominent longitudinal ridges per valve, not counting the ridge which produces the keel of the ventro-lateral margin. Lateral surface coarsely ornamented by a series of pits, grooves and complimentary ridges aligned parallel to the ventro-lateral and terminal margins. Particularly in the female, there is a deep vertical sulcus developed about valve centre. **Normal pore canals** few in number, large and widely spaced. Left valve larger than the right, which it overlaps noticeably along the ventral margin, and both antero- and postero-dorsally. Anteriorly the left valve projects slightly beyond the right and strongly over-reaches dorsally. **Hinge** entomodont. Left valve with coarsely loculate terminal sockets (8 loculi anteriorly and 7 posteriorly), median bar dentate, more coarsely so in anterior half. Accommodation groove broad and rather shallow. Right valve with 8 anterior teeth and 7 posterior teeth; median groove loculate, expanded anteriorly. **Muscle scars** of type **A**. The antero-dorsal antennal scar is quite large in the single specimen showing it, and appears to be formed by a fusion of two smaller, round, scars. Antero-ventral scar round, also larger than the four round adductor scars which are arranged in a slightly crescentic row. **Inner margin** and **line of concrescence** coincide, the **duplicature** being rather narrow. As a result the widely spaced, straight, **radial pore canals** are rather short. Anteriorly there are 8 whilst posteriorly only 3.

Dimensions. Holotype. Io.2434, female carapace, length 0·72 mm.; height 0·49 mm.; width 0·42 mm.

Paratypes. Io.2435, male carapace, length 0·80 mm.; height 0·49 mm.; width 0·39 mm. Io.2436, female right valve, length 0·63 mm.; height 0·40 mm. Io.2437, male left valve, length 0·74 mm.; height 0·46 mm. Io.2438, female right valve, length 0·65 mm.; height 0·40 mm.

Remarks. *Progonocythere rugosa* sp. nov. is distinguishable from other species of the genus by the type and coarseness of the ornamentation which in many ways is similar to that often found in species of *Glyptocythere*. However, as with other species of *Progonocythere*, the absence of a dorsomedian projection in the right valve prevents this species being a *Glyptocythere*. It is, in all other details, typical of the genus in which it has been placed.

Progonocythere triquetra sp. nov.

(Pl. 12, figs. 10–13, Pl. 13, figs. 1, 3–9)

DIAGNOSIS. *Progonocythere* with high domed, sub-triangular carapace in female; elongate-subrectangular carapace in male. Both dimorphs in dorsal view have steeply angled lateral surfaces only slightly convex. Ventro-lateral margin extended below ventral surface. Ventral surface ornamented by longitudinal ridges; lateral surface punctate, over which are widely scattered a number of large, circular, normal pore canal openings. Internal details as for genus.

HOLOTYPE. Io. 2453, female carapace, bed J, Kings Cliffe.

PARATYPES. Io. 2454–63, male and female single valves and female carapace from beds H & J, Kings Cliffe and bed H, Ketton.

DESCRIPTION. **Carapace** sub-triangular in the female dimorph having a high domed dorsal outline (left valve) with steeply angled dorsal margins. The male dimorph is much more rectangular in outline and does not possess the high dorsal outline of the female. Greatest length of carapace passes through mid-point with the greatest height at the anterior cardinal angle and greatest width median. Anterior broadly rounded, posterior triangular with concave postero-dorsal slope and convex postero-ventral slope. Dorsal margin very slightly convex, only gently sloping to the posterior in all valves other than the female left valve where it is steeply angled. Antero-dorsal slope convex and short, again in all valves other than in the female left valve where it is long, due to the situation of the anterior cardinal angle only just anterior of valve centre. Ventro-lateral margin strongly convex and extended below the ventral surface. Ventral margin incurved antero-medially, only very shallow in the male left valve and with a ventral " lip " in the right valve. Ventral surface of each valve ornamented by 4–5 longitudinal ridges. Lateral surface punctate. **Normal pore canal** openings widely scattered, large, circular and comparatively few in number. Left valve larger than the right which it overlaps along the ventral surface, in the region of the cardinal angles but strongly over-reaches mid-dorsally. **Hinge** entomodont. Left valve with terminal loculate sockets and a dentate median bar, the dentations being much coarser in the anterior half, above which is an elongate, deep, accommodation groove. Right valve with 6 anterior teeth and 7 posterior teeth in both males and females. All teeth are dorsally bifid. Median groove strongly loculate and expanded anteriorly. **Inner margin** and **line of concrescence** coincide. **Duplicature** narrow; **selvage** prominent. A narrow **flange** extends around the anterior and posterior margins and along the ventral margin in which region it forms the ventral " lip " below the median incurvature. The flange is only clearly seen in the right valve of both dimorphs. **Radial pore canals** short, straight and widely spaced, 8 anteriorly. **Muscle scars**, type A. Adductor scars oval, aligned in a slightly crescentic row with a round antero-dorsal antennal scar and a round antero-ventral mandibular scar.

DIMENSIONS. Holotype Io. 2453, female carapace, length 0·75 mm.; height 0·54 mm.; width 0·40 mm.

Paratypes. Io.2454, female left valve, length 0·62 mm.; height 0·45 mm. Io.2455, female right valve, length 0·66 mm.; height 0·40 mm. Io.2456, male left valve, length 0·86 mm.; height 0·50 mm. Io.2457, male right valve, length 0·70 mm.; height 0·37 mm. Io.2458, female carapace, length 0·79 mm.; height 0·55 mm.; width 0·38 mm.

REMARKS. The subtriangular carapace in the female and the steeply sloping lateral sides when viewed dorsally readily distinguish this species from others of the genus.

Genus ***GLYPTOCYTHERE*** Brand & Malz 1962

REMARKS. The genus first appeared in print in Brand & Malz 1962*a* when 7 species of *Glyptocythere* were described. The diagnosis of the genus and the erection of a type species was not published until a short while later in Brand & Malz 1962*b*.

Glyptocythere guembeliana (Jones)

(Pl. 13, figs. 10–16, Pl. 14, figs. 1–8)

1884 *Cythere guembeliana* Jones : 772, pl. 34, figs. 32, 33 [*non* fig. 31].
1888 *Cytheridea pulvinar* Jones & Sherborn : 266, pl. 3, fig. 2*a–c*.

DIAGNOSIS. *Glyptocythere* with subquadrate carapace, elongate in male dimorph. Lateral surface with transverse ridges extending down from dorsal margin although generally poorly developed in most specimens. Marginal borders compressed. Ventro-lateral margin evenly convex in female, sharply directed upwards posteriorly in male right valve; may possess deep longitudinal groove in either dimorph or may possess short blade-like extension. Hinge weakly entomodont.

LECTOTYPE. Selected here, IN.43493, male right valve, Great Oolite, Richmond boring at a depth of 1205 ft., figured Jones 1884, pl. 34, fig. 33.

PARALECTOTYPE. Io.3338, male carapace from Richmond boring, depth 1205 ft.

JONES'S COLLECTION. I.1858, lectotype of *Cytheridea pulvinar* from the Blue Fullers Earth Clay; Midford, Bath. A female right valve. Figured Jones & Sherborn 1888, pl. 3, fig. 2*a–c*; Io.2464, male right valve fragment from the Blue Fullers Earth Clay; Midford Bath.

OTHER MATERIAL. Io.2465–2512, male and female valves and carapaces from beds F, O & R, Kings Cliffe; beds H & L, Ketton and bed U, Ancaster.

DESCRIPTION. **Carapace** somewhat variable in size, subquadrate in the female, more elongate in the male. Greatest length of carapace passes through mid-point whilst the greatest height median or at the anterior cardinal angle. Greatest width behind mid-point. Anterior broadly rounded in the left valve, tending to develop a short, slightly concave antero-dorsal slope in the right valve. Posterior triangular with a strongly concave, short, postero-dorsal slope and a longer, convex, postero-ventral slope. Ventro-lateral margin broadly convex, obliquely angled posteriorly in the male right valve. Ventral margin with a median incurvature. Dorsal margin strongly convex medially in the right valve, less obviously so in the left. Cardinal angles prominent. Shell surface punctate and generally poorly ornamented though some specimens may develop quite prominent transverse ridges which extend downwards to die out at a line drawn through mid-point. A broad, shallow depression is most noticeably developed in the right valve just behind the anterior cardinal angle. A short blade-like crest may be developed in some specimens on the ventro-lateral margin, whilst others may develop a short but deep, longitudinal groove, just above the ventro-lateral margin. **Normal pore canals** with large, circular openings evenly spaced over the carapace. Left valve larger than the right which it overlaps along the ventral margin and slightly along the antero-dorsal slope. Elsewhere, along the dorsal margin the left valve over-reaches the right. **Hinge** very poorly entomodont. Left valve with terminal, elongate, loculate sockets between which is a strong, coarsely dentate median bar, the teeth of which show a tendency in the anterior portion to become partially united in pairs. Accommodation groove poorly represented. Right valve with 6 anterior and 7 posterior, dorsally bifid, teeth. Median groove coarsely loculate, expanded very slightly in the anterior portion. **Inner margin** and **line of concrescence** coincide. **Duplicature** of moderate width with anteriorly 8, straight and widely spaced **radial pore canals** and 3 posteriorly, 2 of which are situated together at the point of the posterior margin. **Muscle scars** of type **A** with the antero-dorsal antennal scar being much larger than any of the adductors.

DIMENSIONS. Lectotype. IN.43493, male right valve, length 0·96 mm.; height 0·49 mm. Paralectotype. Io.3338, male carapace, length 0·71 mm.; height 0·36 mm.; width 0·32 mm.

Other material. I.1858, female right valve, length 0·82 mm.; height 0·47 mm. Io.2465, male left valve, length 0·71 mm.; height 0·37 mm. Io.2466, male right valve, length 0·83 mm.; height 0·42 mm. Io.2467, female left valve, length 0·70 mm.; height 0·45 mm. Io.2468, female right valve, length 0·72 mm.; height 0·42 mm. Io.2469, female right valve, length 0·66 mm.; height 0·39 mm. Io.2471, male carapace, length 0·73 mm.; height 0·40 mm.; width 0·36 mm. Io.2472, female right valve, length 0·78 mm.; height 0·45 mm. Io.2473, female carapace, length 0·73 mm.; height 0·46 mm.; width 0·39 mm.

REMARKS. Apart from the paralectotype, all specimens from the Jones collection are larger than those of the same sex present within the Upper Estuarine Series. That a male dimorph (the paralectotype) of small size occurs with larger specimens suggests that the adult size of this species is somewhat variable. Also variable within a population is the tendency in some specimens to develop a deep groove near to the ventro-lateral margin and in others for the ventro-lateral margin to be thickened or extended into a blade-like keel. The ornamental features of this species readily identify it from existing species of the genus.

The two species placed in synonymy are simply male and female dimorphs; Jone's *Cythere guembeliana* being the male and *Cytheridea pulvinar* described by Jones & Sherborn, the female.

Glyptocythere juglandica (Jones)

(Pl. 14, fig. 9)

1884 *Cythere juglandica* Jones ; 766, 768, pl. 34, figs. 36, 37.
1888 *Cythere juglandica* var. *major* Jones & Sherborn : 255, pl. 4, fig. *2a–b*.
1948 *Progonocythere juglandica* (Jones) Sylvester-Bradley : 193, pl. 12, figs. 5, 6, pl. 13, fig. 8.
1963 *Progonocythere juglandica juglandica* (Jones) ; Grekoff : 1731, pl. 3, fig. 55.
1963 *Progonocythere? juglandica* (Jones) ; Oertli, pls. 28, 29, 30.

Material. Io.2513–17, male and female carapaces and a female left valve from beds N, O & S, Kings Cliffe.

Remarks. The strong ornamentation and characteristic mid-dorsal extension of the right valve places this species within the genus *Glyptocythere*. The doubtful position of *juglandica* within *Progonocythere* has been noted by Oertli (1963).

Genus ***KLIEANA*** Martin 1940

Klieana levis Oertli

(Pl. 14, figs. 10–13, Pl. 15, figs. 1–5)

1957 *Klieana levis* Oertli : 760, pl. 22, figs. 13–19.

Material. Io.2518–36, male and female carapaces and single valves from bed Q, Kings Cliffe; bed U, Ancaster and bed L, Kettering.

Remarks. Due to the kindness of Dr. Oertli, I have been able to examine some of the material originally described, and to compare it with the present material. The specimens of *Klieana levis*, which are found, often in fairly large numbers, within the Upper Estuarine Series tend to be slightly larger than those described by Oertli, which have an average length of 0·50–0·60 mm., and possess a punctate rather than a smooth carapace. All the specimens figured by Oertli are female dimorphs when compared with the present material and as he states (p. 760) that dimorphism is not recognized with certainty it is probable that the male dimorphs, which are never very common, were not found in the French material. The male dimorph is a very noticeable form much more elongate than the female and does not have the strongly arched dorsal margin to the left valve. The **muscle scars**, not observed in Oertli's material, are of type **A**. **Radial pore canals** straight and widely spaced, 8 anteriorly and 4 posteriorly. **Hinge** antimerodont.

Dimensions. Io.2518, female carapace, length 0·61 mm.; height 0·40 mm.; width 0·32 mm. Io.2520, female right valve, length 0·63 mm.; height 0·39 mm. Io.2521, female left valve, length 0·66 mm.; height 0·43 mm. Io.2522, male carapace, length 0·74 mm.; height 0·36 mm.; width 0·35 mm.

Genus ***LOPHOCYTHERE*** Sylvester-Bradley 1948

Lophocythere ostreata (Jones & Sherborn)

1888 *Cytheridea ostreata* Jones & Sherborn : 271, pl. 4, fig. 6.
1948 *Lophocythere ostreata* (Jones & Sherborn) Sylvester-Bradley : 195, pl. 14, figs. 1–4, pl. 15, figs. 1, 2.

REMARKS. A single, juvenile carapace (Io.2540) found in bed S, Kings Cliffe. Not figured.

Lophocythere scabra scabra Triebel

(Pl. 15, fig. 6)

1951 *Lophocythere scabra* Triebel : 95, pl. 46, figs. 26–30, pl. 47, figs. 31–34.
1960 *Lophocythere scabra scabra* Triebel ; Lutze : 429, pl. 37, fig. 1.
1962 *Lophocythere scabra scabra* Triebel ; Brand & Fahrion : 147, pl. 21, fig. 32.
1963 *Lophocythere scabra* Triebel ; Oertli : 43, pls. 26, 28–30.

MATERIAL. Io.2537–39 and Io.2541, male and female valves and carapaces from beds F & R, Kings Cliffe.

REMARKS. Like *Glyptocythere juglandica*, *Lophocythere scabra scabra* is a typical Bathonian ostracod and is common in the majority of the marine sediments of the Upper Estuarine Series.

Lophocythere septicostata sp. nov.

(Pl. 15, figs. 7–13, Pl. 16, figs. 1–4)

1888 *Cytheridea bradiana* Jones & Sherborn : 272, pl. 4, figs. 11*a–c*.

DIAGNOSIS. *Lophocythere* having seven longitudinal ridges on lateral surface and two on ventral surface. A vertical ridge extends downwards from oval eye swelling. Interspaces between ridges, punctate, with large, circular, normal pore canal openings. Anterior and posterior marginal borders compressed.

HOLOTYPE. Io.2542, female carapace from bed B, Kettering.

PARATYPES. Io.2543–49, male and female carapaces and male left valve from bed B, Kettering; bed V, Ancaster and bed N, Kings Cliffe. I.1843, female right valve, described by Jones & Sherborn as *Cytheridea bradiana* figd., pl. 4, figs. 11*a–c*, from the Blue Fullers Earth Clay; Midford, Bath. Eight male and female specimens (Io.3600–07) of the Möckler collection from the Fullers Earth; Midford nr. Bath.

DESCRIPTION. **Carapace** subquadrate in the female dimorph, elongate in the male. Greatest length passes through mid-point whilst greatest height occurs at the anterior cardinal angle in the female, posteriorly in the male. Greatest width in the posterior third. The carapace possesses prominent, well rounded cardinal angles with the dorsal margin between tending to be medially concave in the left valve, gently convex in the right. The ventral margin is incurved medially whilst the ventral surface is overhung by the convex ventro-lateral margins. Anterior high, broadly rounded; posterior triangular with concave postero-dorsal slope and convex postero-ventral slope. Anterior and posterior marginal borders compressed in the female, only posteriorly so in the male. Shell surface laterally ornamented by a series of 7 oblique, longitudinal ridges which in the anterior half bend downwards and fuse together so that only 2 ridges extend as far as the antero-ventral margin.

The median ridges tend to be short but one of these is long and extends to the antero-ventral margin, although it is not always the same ridge in each specimen which does this. An oval **eye swelling**, situated below the anterior cardinal angle, has a prominent ridge extending from it as far as the uppermost of the two ridges. Surface of carapace between the ridges is punctate and in some specimens also seen to possess large, circular **normal pore canal** openings. Ventral surface possesses two further longitudinal ridges. Left valve larger than the right which it overlaps along the ventral margin and slightly at the cardinal angles. Elsewhere dorsally, the left overreaches the right. **Hinge** entomodont, left valve not clearly seen but in the right there are 5 anterior teeth and 6 posterior teeth, the coarsely loculate median groove being noticeably expanded in its anterior portion. **Inner margin** and **line of concrescence** coincide, no **radial pore canals** observed. A narrow **flange** extends around the anterior margin and continues much reduced outside the ventral margin. **Muscle scars** not observed.

DIMENSIONS. Holotype. Io.2542, female carapace, length 0·72 mm.; height 0·40 mm.; width 0·34 mm.

Paratypes. I.1843, female right valve (Jones & Sherborn colln.) length 0·64 mm.; height 0·33 mm. Io.2546, female carapace, length 0·72 mm.; height 0·43 mm.; width 0·35 mm. Io.2547, male carapace, length 0·77 mm.; height 0·36 mm.; width 0·35 mm.

REMARKS. Jones (1884 : 772) described a new ostracod species named *Cythere bradiana*, subsequently placed into *Lophocythere* by Sylvester-Bradley (1948 : 196). Jones & Sherborn (1888) described material from the Fullers Earth near Bath and identified some specimens as belonging to *Cythere bradiana* although they changed the generic name to *Cytheridea* without comment. This material was not, however, conspecific with their earlier *Cythere bradiana* although like that species, belongs in the genus *Lophocythere*. Jones & Sherborn's material is included here in the new species *Lophocythere septicostata*. *L. septicostata* differs from *L. bradiana* in the number of lateral ridges and absence of reticulation between (although a single male carapace, Io.2547, shows some evidence of reticulation), characters which also serve to distinguish the present species from *L. multicostata* Oertli (1957 : 667). In addition, the compressed anterior marginal border present in the female dimorph of *L. septicostata* distinguishes this species in dorsal view from the other two species. The possession of an eye swelling identifies this species as belonging to the genus *Lophocythere* rather than to the related genus *Terquemula* Blaszyk & Malz 1965.

Lophocythere transversiplicata sp. nov.

(Pl. 16, figs. 5–15)

DIAGNOSIS. *Lophocythere*, with three primary longitudinal ridges; secondary transverse ridges radiating down from ridge to produce broad reticulation between longitudinal ridges. All three longitudinal ridges converging towards antero-ventral margin. Minor transverse ridge extending down from region of anterior cardinal angle. Ventral surface also ornamented with longitudinal ridges.

HOLOTYPE. Io. 2625, female carapace, bed J, Ketton.

PARATYPES. Io. 2626–29, 3087–89, male and female carapaces and single valves, bed J, Ketton.

DESCRIPTION. **Carapace** subquadrate to subrectangular, the more elongate specimens being the males. Anterior high and broadly rounded; posterior triangular with concave postero-dorsal slope and convex postero-ventral slope. Anterior cardinal angle, through which passes the line of greatest height, prominent; the right valve has a low **eye swelling** situated below. Posterior cardinal angle not so prominent as the anterior angle. Dorsal margin of left valve overreached strongly by an extension of the valve. Ventral margin incurved antero-medially. Greatest length of carapace passes through mid-point whilst the greatest width lies in the posterior third. Ventral surface ornamented by four prominent longitudinal ridges per valve. Lateral surface with three longitudinal ridges which converge towards the antero-ventral margin. The dorsal ridge also bends down posteriorly to join the median ridge below. A series of minor transverse ridges extend down from the dorsal ridge and produce a coarse reticulation between the longitudinal ridges. In addition a transverse ridge extends down from the region of the anterior cardinal angle to fuse with the three longitudinal ridges. Left valve is larger than the right which it overlaps along the ventral margin and slightly at the cardinal angles. Dorsally the left over-reaches the right. **Hinge** entomodont. Left valve with terminal loculate sockets, virtually no accommodation groove and a dentate median bar. Because of damage to this bar, the typical entomodont character cannot be seen. Right valve with 5 anterior and 6 posterior teeth. Median groove loculate, expanded in the anterior half. **Inner margin** and **line of concrescence** coincide. **Radial pore canals** straight, 9 anteriorly and 4 posteriorly. Other internal details not observed.

DIMENSIONS. Holotype. Io. 2625, female carapace, length 0·56 mm.; height 0·34 mm.; width 0·31 mm.

Paratypes. Io. 2626, male carapace, length 0·70 mm.; height 0·34 mm.; width 0·31 mm. Io. 2627, female right valve, length 0·53 mm.; height 0·28 mm. Io. 2628, male right valve, length 0·68 mm.; height 0·27 mm. Io. 2629, male left valve, length 0·62 mm., height 0·32 mm.

REMARKS. *Lophocythere transversiplicata* sp. nov. bears some resemblances to *L. flexicosta* Triebel (1951 : 97, pl. 48, figs. 46–48) and *L. plena* Triebel (1951 : 100, pl. 49, figs. 60–63) but differs from both in not having such a neat reticulate ornamentation over the lateral surface. The reticulation that does occur being produced simply by branching and anastomosing transverse ridges restricted to the interspaces between the longitudinal ridges and not generally present over the entire lateral surface. It is distinguished from species of *Terquemula* Blaszyk & Malz 1965 on ornamentation and possession of an eye swelling.

Genus *MACRODENTINA* Martin 1940

Remarks. Malz (1958) erected three subgenera for the genus, namely:—

***Macrodentina* (*Dictyocythere*)**

***Macrodentina* (*Macrodentina*)**

***Macrodentina* (*Polydentina*)**

Each subgenus is identified by the type of amphidont hinge present, in all cases the median element being smooth. The first appearance of the genus according to the present literature occurs towards the base of the Upper Jurassic (Kimmeridge). Within the Upper Estuarine Series, however, there is found, often in large numbers, a species of ostracod which undoubtedly belongs to the genus *Macrodentina*. Here the hinge is a much more primitive type with a dentate/loculate median element. This form extends the range of the genus down into the Middle Jurassic and a new subgenus, *Mediodentina*, is erected to contain it.

Subgenus *MEDIODENTINA* nov.

Diagnosis. *Macrodentina* with entomodont hinge. Other details as for genus.

Type species. *Macrodentina* (*Mediodentina*) *bathonica* sp. nov.

Macrodentina (*Mediodentina*) *bathonica* sp. nov.

(Pl. 17, figs. 1–12, Pl. 18, figs. 1–4)

Diagnosis. *Mediodentina* having sub-quadrate to sub-rectangular carapace with prominent cardinal angles. Tendency to develop small marginal denticles antero- and postero-ventrally. Dimorphic. Shell surface strongly punctate with large, circular, normal pore canal openings. Punctation may be so well developed as to produce almost reticulate type ornamentation.

Holotype. Io.2550, female carapace, bed Q, Kings Cliffe.

Paratypes. Io.2551–72, male and female carapaces and single valves from beds J, Q & R, Kings Cliffe and bed L, Ketton.

Description. **Carapace** subquadrate in the female dimorph, sub-rectangular in the more elongate male dimorph. Greatest length in both sexes passes through mid-point with the greatest height through the anterior cardinal angle and the greatest width in the posterior third. Anterior high, broadly rounded; posterior quite broad and also rounded, although the short, almost vertical postero-dorsal slope gives a concavity just below the posterior cardinal angle. Both cardinal angles are prominent but the posterior one is especially so. Dorsal margin slightly convex in the female and with a very shallow concavity behind the anterior cardinal angle. In the male these features are more strongly exaggerated. Ventro-lateral margin convex, overhanging the ventral surface. Ventral margin antero-medially incurved. Left valve larger than the right which it overlaps along the ventral margin. In the region of the antero- and postero-dorsal slopes the valve relationship is one of over-reach rather than overlap. Shell surface strongly punctate, the punctation in a single specimen almost giving rise to reticulation—the punctae being enlarged almost to size of pits. **Normal pore canal** openings are large and circular and both evenly and widely spaced over the carapace. Small marginal denticles are commonly developed in the postero-ventral and antero-ventral regions. **Hinge** strongly entomodont. Left valve with oval, coarsely loculate terminal sockets and a coarsely dentate median bar, the denticles being greatly enlarged in the anterior portion. Accommodation groove shelf-like, though rather narrow, particularly in the male dimorph. Right valve with 6 anterior and 6 posterior, dorsally bifid, teeth. Median groove coarsely loculate and greatly expanded in its anterior half. **Inner margin** and **line of concrescence** coincide, **duplicature** being of moderate width. Anterior **radial pore canals** 8 in number, straight and widely spaced; only 2–4 posteriorly. Right valve has a prominent " lip " developed just below the median incurvature. **Muscle scars** of type **A**. The four adductor scars are rather small as is the round antennal scar which is antero-dorsal in position.

DIMENSIONS. Holotype. Io.2550, female carapace, length 0·86 mm.; height 0·51 mm.; width 0·42 mm.

Paratypes. Io.2551, male carapace, length 0·85 mm.; height 0·45 mm.; width 0·37 mm. Io.2552, male left valve, length 0·85 mm.; height 0·46 mm. Io.2553, male left valve, length 0·95 mm.; height 0·51 mm. Io.2554, female left valve, length 0·84 mm.; height 0·54 mm. Io.2555, immature female left valve, length 0·65 mm.; height 0·40 mm. Io.2556, female right valve, length 0·68 mm.; height 0·43 mm. Io.2558, juvenile left valve, length 0·67 mm.; height 0·41 mm. Io.2559, juvenile right valve, length 0·61 mm.; height 0·38 mm.

REMARKS. In some ways this species resembles the ostracod Indet. genus sp. *A*. Oertli (1957 : 676) but may be distinguished by the possession of more prominent cardinal angles, especially posteriorly, and the convexity of the ventro-lateral margin. None of these features is particularly well developed in Oertli's material.

Genus ***MARSLATOURELLA*** Malz 1959

Marslatourella bullata sp. nov.

(Pl. 18, figs. 5–14, Pl. 19, figs. 1, 2)

DIAGNOSIS. *Marslatourella* with subquadrate carapace; prominent eye node with short vertival ridge extending ventrally from it. Ventro-lateral margin with two knob-like extensions. Shell surface punctate with anterior denticles. A small " lip " of right valve overlaps left mid-ventrally. Carapace equivalve.

HOLOTYPE. Io.2573, right valve from bed H, Ketton.

PARATYPES. Io.2574–81, single valves and complete carapaces from beds H & N, Ketton; bed R, Kings Cliffe and bed J, Kettering.

DESCRIPTION. **Carapace** subquadrate with well rounded anterior; rounded-triangular posterior; straight dorsal margin with acute cardinal angles and strongly concave (medially) ventral margin. Male dimorph slightly more elongate than the female for a given height. Greatest length passes through mid-point with the greatest height situated at the anterior cardinal angle. Greatest width median. The carapace here is equivalve with the left and right valves fitting side by side. The left valve very slightly projects beyond the right terminally whilst mid-ventrally, a small " lip " of the right valve overlaps the left. A narrow **flange** extends around the free margin of each valve and especially around the anterior is broken up into a number of small denticles. Shell surface punctate. Ventro-lateral margin extended into 2 prominent knob-like processes which terminally tend to flatten out and become blade-like. **Eye node** prominent at the anterior cardinal angle with a short, straight ridge extending ventrally from it. **Normal pore canal** openings small and rather numerous. **Hinge** delicately antimerodont. Left valve with a long, finely denticulate median bar and small terminal sockets which appear to be ventrally open to the interior of the valve. Right valve with a long narrow groove, presumably locellate and finely dentate terminal ridges, the exact number of teeth involved not determined. **Inner margin** and **line of concrescence** coincide, **radial pore canals** straight, rather thin and well spaced, approximately 16 anteriorly and 6 posteriorly. **Muscle scars** as seen through the carapace appear to be of type **A**, the antero-dorsal antennal scar being round.

DIMENSIONS. Holotype. Io.2573, female right valve, length 0·68 mm.; height 0·39 mm.

Paratypes. Io.2575, male carapace, length 0·78 mm.; height 0·41 mm.; width 0·34 mm. Io.2578, female left valve, length 0·69 mm.; height 0·40 mm. Io.2579, female carapace, length 0·77 mm.; height 0·43 mm.; width 0·37 mm.

REMARKS. *M. bullata* sp. nov. is larger than the type species (*M. exposita* Malz 1959 : 20) of which Dr. Malz kindly sent me material for comparison purposes. *M. exposita* has an average length of 0·51–0·59 mm. *M. bullata* further differs from the type species in the form of the ventro-lateral outgrowths which are knob-like rather than alate and in its more rounded posterior. The denticulate flange, especially around the anterior margin is a further distinguishing feature of this species.

Genus ***MICROPNEUMATOCYTHERE*** Bate 1963

Micropneumatocythere postrotunda sp. nov.

(Pl. 19, figs. 3–10, 13–16)

DIAGNOSIS. *Micropneumatocythere* having ovoid rather tumid carapace; arched dorsal outline; broadly rounded posterior; more narrowly rounded anterior. Shell surface punctate with 3 longitudinal ridges extending along ventral surface of each valve. Normal pore canal openings fairly large. Low swelling occurs just below anterior cardinal angle. Internal details as for genus.

PARATYPES. Io.2583–91, single valves and carapaces from beds J, P & R, Kings Cliffe.

HOLOTYPE. Io.2582, carapace, bed P, Kings Cliffe.

DESCRIPTION. **Carapace** tumid, ovoid in outline with terminally flattened broadly rounded posterior and a more narrowly rounded blunted anterior. Dorsal margin arched with rounded cardinal angles. Ventro-lateral margin medially swollen, overhanging the ventral surface in lateral view. Ventral margin incurved antero-medially. Greatest length of carapace passes through mid-point with both the greatest length and width median. Shell surface very finely punctate with widely spaced normal pore canals prominent. Ventral surface of carapace weakly ridged. A low swelling below the anterior cardinal angle may represent an **eye swelling**. Left valve overlaps the right along the ventral margin but diverges away from the right as it approaches the anterior where there is no overlap. Posteriorly, however, the overlap by the left valve continues round to the posterior cardinal angle. Dorsally the left valve over-reaches the right. **Hinge** antimerodont. Left valve with elongate loculate terminal sockets and a long, denticulate median bar, above which there is a shallow accommodation groove. Right valve with 7 posterior teeth and 6 anterior teeth. All the teeth are dorsally bifid. Median groove locellate. **Inner margin** and **line of concrescence** coincide, the **duplicature** being rather narrow. **Radial pore canals** short and thick, widely spaced; 8 anteriorly, 4 posteriorly. **Muscle scars** of type **A**, situated fairly low down in the anterior part of the carapace. The 4 adductor scars are situated in a subvertical row with the most dorsal scar being slightly offset to the anterior. Antennal scar large, round and antero-dorsal in position. The round mandibular scar has an antero-ventral position.

DIMENSIONS. Holotype. Io.2582, carapace, length 0·60 mm.; height 0·41 mm.; width 0·33 mm.

Paratypes. Io.2583, carapace, length 0·64 mm.; height 0·44 mm.; width 0·34 mm. Io.2584, left valve, length 0·64 mm.; height 0·43 mm. Io.2585, left valve, length 0·56 mm.; height 0·38 mm. Io.2586, right valve, length 0·49 mm.; height 0·32 mm.

REMARKS. *Micropneumatocythere postrotunda* sp. nov. is easily distinguishable from all other species of the genus by its well rounded somewhat flattened posterior and blunt, narrower anterior. Dimorphism has not been observed for this species.

Micropneumatocythere quadrata sp. nov.

(Pl. 19, figs. 11, 12, Pl. 20, figs. 1–12.)

DIAGNOSIS. *Micropneumatocythere*, with sub-quadrate rather deep carapace (elongate in male dimorph); cardinal angles prominent, especially posterior angle. Postero-dorsal slope steeply angled; postero-ventral slope characteristically broad, deep, strongly convex. Shell surface punctate with widely spaced, large, normal pore canals. Internal details as for genus.

HOLOTYPE. Io.2592, female carapace, bed P, Kings Cliffe.

PARATYPES. Io.2593–2606, male and female carapaces and single valves from beds F, O, P, R & S, Kings Cliffe.

DESCRIPTION. **Carapace** subquadrate with high, arched dorsal outline in the female dimorph, elongate in the male. Cardinal angles especially the posterior angle sharply defined, the anterior angle in the left valve is, however, broadly rounded. Anterior broadly rounded, posterior triangular and slightly upturned at extremity. Dorsal margin more strongly convex in the left valve than in the right. Antero-dorsal slope broadly convex; postero-dorsal slope steep, slightly concave in the left valve but more strongly so in the right. Postero-ventral slope broadly convex. Ventral margin antero medially incurved. Ventro-lateral margin typically swollen and overhanging the ventral surface in lateral view. Posterior border compressed at extremity. Greatest length of carapace passes through mid-point, whilst both greatest height and width are median. Shell surface finely punctate, over which large **normal pore canal** openings are scattered. Ventral surface with 4–5 longitudinal ridges per valve. Left valve larger than the right which it overlaps along the ventral margin except medially where a small section of the right valve slightly overlaps the left. Around the anterior and along the antero-, and postero-dorsal slopes the left valve slightly over-reaches the right. Mid-dorsally, however, the over-reach of the right valve by the left is very strong, the elongate, triangular accommodation groove of the left valve being completely visible. **Hinge** antimerodont. Left valve with elongate, loculate terminal sockets, a strong, dentate median bar and an elongate triangular accommodation groove. Right valve with 6 (dorsally bifid) anterior teeth and 7, also bifid, posterior teeth. Median groove loculate. **Inner margin** and **line of concrescence** coincide; **duplicature** of moderate width. **Radial pore canals** few in number, widely spaced and tend to widen towards the inner margin. 7–8 anteriorly; approximately 3 posteriorly. **Muscle scars** not observed.

DIMENSIONS. Holotype. Io.2592, female carapace, length 0·56 mm.; height 0·39 mm.; width 0·35 mm.

Paratypes. Io.2593, male carapace, length 0·68 mm.; height 0·41 mm.; width 0·37 mm. Io.2594, female right valve, length 0·61 mm.; height 0·38 mm. Io.2595, female left valve, length 0·55 mm.; height 0·40 mm. Io.2596, female carapace, length 0·56 mm.; height 0·41 mm.; width 0·37 mm.

REMARKS. *Micropneumatocythere quadrata* sp. nov. is distinguished from all other species of the genus by the sharply angled posterior cardinal angle coupled with the broad, deep, postero-ventral slope. Although tending to vary with individuals, the left valve rather more strongly overreaches the right valve than is usual for the genus.

Micropneumatocythere subconcentrica (Jones)

(Pl. 21, figs. 1–13)

1884 *Cythere subconcentrica* Jones : 768, pl. 34, figs. 28, 29.

DIAGNOSIS. *Micropneumatocythere* with oval carapace, tapering to posterior. Ventro-lateral margin swollen. Shell surface punctate laterally. Ventral surface with longitudinal ridges extending onto ventro-lateral margin and turning upwards anteriorly and posteriorly. Internal details as for genus.

LECTOTYPE. Selected here. In.43505, left valve, Great Oolite; Richmond boring at depth of 1,151 ft. 6 in. figured Jones 1884, pl. 34, fig. 28. Although Jones refers to his fig. 28 as being of a right valve, the illustration appears to be a left valve. Specimen In.43505 is considered to be the one illustrated.

OTHER MATERIAL. Io.2606–12, carapace and single valves from bed F, Kings Cliffe and bed H, Ketton.

DESCRIPTION. **Carapace** ovoid with arched dorsal outline and rounded cardinal angles. Posterior tapering, slightly rounded with concave postero-dorsal slope and convex postero-ventral slope. Ventro-lateral margin swollen projecting below ventral surface in side view. Anterior rounded. Ventral margin antero-medially incurved. Line of greatest length passes through mid-point, greatest height and width median. Shell surface laterally punctate, ventrally ridged, the ridges passing onto the ventro-lateral margin and sub-concentrically turn upwards anteriorly and posteriorly. This rather weak ornamentation rapidly dies out upwards. **Normal pore canals** are widely spaced over the carapace, their openings being rather large and circular. Left valve larger than the right which it overlaps along the ventral margin except for a small median section where the right valve overlaps the left. Dorsally the left valve over-reaches the right. **Hinge** antimerodont. Left valve with elongate, loculate, terminal sockets, a denticulate median bar and a deepish accommodation groove. Right valve with approximately 5–6 terminal teeth and a long, delicate, locellate groove. **Muscle scars** of type **A**, the small, round, antennal scar having an antero-dorsal position. **Inner margin** coincides with the **line of concrescence** apart from antero-medially where a very narrow **vestibule** may be present, but not in all cases. **Radial pore canals** few in number, straight and widely spread, 7 anteriorly, 3 posteriorly. A narrow **flange** may be preserved around the anterior margin but as this is a very delicate structure it is usually lost.

DIMENSIONS. Lectotype. IN.43505, left valve, length 0·56 mm.; height 0·38 mm. Other material. Io.2607, carapace, length 0·57 mm.; height 0·37 mm.; width 0·32 mm. Io.2608, left valve, length 0·51 mm.; height 0·34 mm. Io.2609, right valve, length 0·49 mm.; height 0·30 mm. Io.2610, left valve, length 0·50 mm.; height 0·34 mm.

REMARKS. *Micropneumatocythere subconcentrica* (Jones) resembles *M. globosa* Bate (1964 : 12) in outline but differs in being a much larger species and in having a more prominent ornamentation of ridges on the ventro-lateral margin. Dimorphism has not been observed for *M. subconcentrica* although it is well developed in *M. globosa*. The close similarity of the two species suggests, however, that the present species is a descendant of *M. globosa*.

Family **TRACHYLEBERIDIDAE** Sylvester-Bradley 1948

Subfamily **TRACHYLEBERIDINAE** Sylvester-Bradley 1948

Genus ***OLIGOCYTHEREIS*** Sylvester-Bradley 1948

Oligocythereis fullonica (Jones & Sherborn)

(Pl. 21, figs. 14, 15)

1888 *Cytheris fullonica* Jones & Sherborn : 256, pl. 4, fig. 13*a–c*.
1948 *Cythereis* cf. *fullonica* Jones & Sherborn ; Sylvester-Bradley : 186, pl. 12, figs. 7–10 ; pl. 13, figs. 3, 9.
1948*a* *Oligocythereis fullonica* (Jones & Sherborn) Sylvester-Bradley : 796, pl. 122, figs. 1–6.
1962 *Oligocythereis* cf. *fullonica* (Jones & Sherborn) ; Brand & Fahrion : 150, pl. 21, fig. 27.
1963 *Oligocythereis fullonica* (Jones & Sherborn) ; Oertli : 41, pl. 25 fig. *a*, pl. 26, fig. *a*.

REMARKS. Only two specimens of this species have been found within the Estuarine Series and these occur in the Ancaster bed W (possibly Gt. Oolite), and Dane Hill sections. Both are ornamentally different. Sylvester-Bradley (1948 : 187) records three varieties within the species but did not have sufficient material to determine whether this was of systematic significance. The same is true here.

Family Uncertain.

Genus ***PLATYCYTHERE*** nov.

DIAGNOSIS. Cytheracea with subquadrate to subrectangular carapace, laterally flattened with thickened overhanging dorsal and ventral areas. Dorsal and ventral surfaces flattened. In dorsal view parallel sided or slightly diverging to venter. Ornamentation strongly to weakly reticulate. Left valve very slightly larger than right. Hinge entomodont, muscle scars type **A**. Inner margin and line of concrescence coincide. Radial pore canals straight, few, widely spaced; 8 anteriorly, 3 posteriorly. Normal pore canals large, few, widely and irregularly scattered over carapace.

TYPE SPECIES. *Platycythere verriculata* sp. nov.

REMARKS. Although possessing characters which identify the genus as belonging to the Cytheracea it is not possible at this stage to place it in any known family. The unusually flattened carapace, provides only a narrow internal space for the animal when closed, whilst the swollen dorsal and ventral parts of the carapace might have had a functional use such as acting as stabilizers whilst crawling over bottom sediment.

Platycythere verriculata sp. nov.

(Pl. 22, figs. 1–13)

DIAGNOSIS. *Platycythere* with subquadrate/subrectangular carapace flattened laterally in dorsal view. Ventro-lateral and dorso-lateral margins swollen, projecting beyond lateral surface. Dorsal and ventral surfaces also flattened. Shell surface coarsely reticulate with smooth marginal border in male dimorph, tending to be smooth entirely in juvenile instars and in female dimorph, although some ornamentation usually observed in region of dorsal and ventral swellings. Ventral surface ornamented with longitudinal ridges in both dimorphs. Internal details as for genus.

HOLOTYPE. Io.2613, male carapace bed J, Kettering.

PARATYPES. Io.2614–22, female and juvenile carapaces and male valves, beds A, G & J, Kettering and bed N, Kings Cliffe.

DESCRIPTION. **Carapace** subquadrate in the female dimorph, elongate, subrectangular in the male. Carapace typically flattened in dorsal view, the sides being parallel in the male but tending to slope outwards towards the venter in the female. Ventro-lateral and dorso-lateral margins swollen, projecting beyond the lateral surface when viewed dorsally. Dorsal and ventral surfaces flattened. The female carapace tapers towards the posterior, whilst the male tends to have dorsal and ventral margins almost parallel. Anterior broadly rounded, posterior rounded, but more narrowly so. The ventral margin has only a very shallow antero-median incurvature; dorsal margin almost straight sloping gently or strongly towards the posterior depending upon the dimorph. Greatest length of carapace extends through mid-point whilst greatest height is approximately median in the female and either at the anterior cardinal angle or just behind middle in the male. Greatest width possibly through middle of carapace in the female, whilst in the male the parallel lateral margins give no point at which the carapace is widest. Shell surface coarsely reticulate in the male dimorph, the reticulations tending to die out towards the anterior and posterior so that an unornamented border is apparent. In the female dimorph and in juvenile instars there is almost no trace of the reticulate ornamentation save in the region of the ventral and dorsal swellings. Ventral surface ornamented with 5–6 longitudinal ridges per valve in both dimorphs. **Normal pore canals** very widely and irregularly scattered over the carapace, few in number and rather large, circular or almost hexagonal in outline. Left valve slightly overlaps the right at the cardinal angles and, particularly in the female slightly projects beyond the right around the anterior and posterior. Ventrally the two valves have neither overlap nor overreach. **Hinge** entomodont. Left valve with elongate terminal sockets, presumably loculate but infilled with matrix, and a long denticulate median bar, the anterior portion of which is very coarsely dentate. No accommodation groove. Right valve with 6 strong anterior teeth and 5 much smaller and weaker posterior teeth. Median groove loculate, expanded and more coarsely loculate in its anterior portion. **Muscle scars** of type A, the four small adductor scars arranged in a slightly crescentic row with the small, round, antennal scar positioned antero-dorsally. Antero-ventrally the mandibular scar is also rounded and is very much larger than those previously described. **Inner margin** and **line of concrescence** coincide; **duplicature** of moderate width, **radial pore canals** straight, few in number and widely spaced, 8 anteriorly and 3 posteriorly.

Dimensions. Holotype. Io.2613, male carapace, length 0·67 mm.; height 0·37 mm.; width 0·30 mm.

Paratypes. Io.2614, male right valve, length 0·66 mm.; height 0·37 mm. Io.2615, male right valve, length 0·54 mm.; height 0·31 mm. Io·2616, male left valve, length 0·66 mm.; height 0·37 mm. Io.2621, female carapace, length 0·60 mm.; height 0·37 mm.; width 0·26 mm. Io.2622, juvenile carapace, length 0·47 mm.; height 0·30 mm.; width 0·19 mm.

Remarks. *Platycythere verriculata* sp. nov. is quite unlike any previously described species and belongs to a distinct genus. The variation present within the species with regard to the ornamentation could suggest the presence of two distinct species. However, the outline of the smooth species suggests that the most probable explanation is that this is the female dimorph, the smaller juvenile instars being similarly without ornamentation. Only in the more elongate male dimorph is the reticulate ornamentation strongly developed over the lateral surface.

The width measurements given above are for the carapace excluding the swollen dorsal and ventral parts and are taken at valve centre.

III. PALAEOECOLOGY

The work undertaken by Aslin has shown there to be a variable and alternating succession of both marine and freshwater sediments exposed along the entire outcrop of the Upper Estuarine Series. The study of the ostracod faunas is, therefore, doubly interesting in that the stratigraphy of the succession has been examined in some detail.

The base of the Upper Estuarine Series is dominated by purplish grey clays with plant remains representing a continental period of deposition. The absence of ostracods from these beds and from the freshwater horizons which return from time to time throughout the succession is almost certainly due to decalcification. The marine horizons are more strongly calcified and contain a good macro- and microfauna, the evidence of which suggests deposition close to land and influenced by river effluent. As such both brackish water and marine ostracods are encountered. Completely freshwater faunas are probably not encountered for the reasons mentioned above, although faunas of low salinity are recorded and represent ostracod populations living some distance upstream from a river mouth or in a more static back swamp body of water. These low salinity populations are represented by the following species: *Darwinula incurva*, *Bisulcocypris ancasterensis*, *Belekocytheridea punctata* and *Macrodentina* (*Mediodentina*) *bathonica* at Ancaster, and at Kings Cliffe by *Darwinula incurva*, *Bisulcocypris anglica*, *Klieana levis*, *Macrodentina* (*Mediodentina*) *bathonica* and *Micropneumatocythere postrotunda*. Both populations are found associated with freshwater-brackish-water charophytes. The two species of *Bisulcocypris* together with *Darwinula incurva* are considered to represent freshwater-oligohaline ostracods whilst the species of *Klieana*, *Macrodentina*, *Belekocytheridea* and *Micropneumatocythere* are considered to be euryhaline and found more typically in brackish water assemblages.

The evidence in support of the freshwater-oligohaline habit of the species mentioned above is as follows:

Firstly, the sediments in which the ostracods were found occur in that part of the rythmic sequence which is subject to the greatest freshwater influence.

Secondly, the ostracod population is restricted in the number of species present and lacks the normal marine ostracods (e.g. *Lophocythere* and *Progonocythere*).

Thirdly, the reported occurrence elsewhere of the ostracod genera concerned by other authors substantiates the findings here. For example *Klieana levis* Oertli (1957 : 760) was originally described from lacustrine sediments from Poitou in France whilst Van Morkhoven (1963 : 268) records the environmental range of the genus as being from fresh to brackish water. *Darwinula* is an essentially freshwater genus with some species ranging into brackish water. The type species, *Darwinula stephensoni* (Brady & Robertson 1870) is living at the present time in rivers and lakes in East Anglia from which area it was originally described. Van Morkhoven (1963 : 29) and Moore (1961 : Q254) give the ecological range of the genus as fresh-brackish water. The genus *Bisulcocypris* is regarded by Pinto & Sanguinetti (1962 : 75) as being typically freshwater. Malz in his excellent work on the genus *Macrodentina* gives the ecological habit of each of the subgenera comprising the genus as being either marine or marine to brackish. The new subgenus *Mediodentina* is considered to have a wide range from marine through brackish to almost freshwater conditions.

In at least two horizons in the Kettering section mixed assemblages of truly marine ostracods such as *Lophocythere scabra*; *Pichottia magnamuris*, *Marslatourella bullata* and *Schuleridea* (*Eoschuleridea*) *bathonica* are found associated with the euryhaline species of *Klieana* and *Macrodentina* and the oligohaline species of *Bisulcocypris* and *Darwinula*. This is not a typical assemblage and results either through the action of rivers bringing into the area ostracods which normally inhabit waters of lower salinity or as is more likely in this case, transgression of marine conditions results in the mixing of faunas, the low salinity ostracods being killed but preserved in the sediments deposited.

The euryhaline ostracods present in the Upper Estuarine Series have been mentioned already but in addition to these a number of normally marine species may also be found under brackish conditions. These are: *Glyptocythere guembeliana*; *Platycythere verriculata* and the two remaining species of *Micropneumatocythere*.

As has been suggested above regions of deposition where periods of marine transgression are common are liable to produce mixed assemblages. Blurring of boundaries between freshwater, brackish water and marine conditions is normal and results in mixing of faunas to some extent. There are, however, four ways in which mixing of ostracod faunas may result.

1. Normal mixing at the boundaries of salinity zones.
2. Freshwater species brought into brackish or marine conditions by rivers.
3. Transgression of the sea flooding bodies of freshwater and bringing marine ostracods into the area.
4. Reworking of sediments whether marine or freshwater and the redeposition of the ostracods present. Thus part of the ostracod fauna would be allochthonous and part autochthonous.

It is more than likely that all four variables have been operative during the deposition of the Upper Estuarine Series.

The ostracod species which appear to be most truly marine throughout are: *Paracypris terraefullonica*; *Monoceratina scarboroughensis*; *Galliaecytheridea? kingscliffensis*; *Pichottia magnamuris*; *Schuleridea* (*Eoschuleridea*) *bathonica*; *Praeschuleridea quadrata*; *Metacytheropteron drupacea*; *Progonocythere levigata*; *P. rugosa* and *P. triquetra*; *Glyptocythere juglandica*; *Lophocythere scabra*; *L. septicostata* and *L. transversiplicata*; *Marslatourella bullata* and *Oligocythereis fullonica*. All the ostracods mentioned as occurring in brackish waters also are found associated with the more restricted marine species listed above. Only *Macrodentina* (*Mediodentina*) *bathonica*, *Belekocytheridea punctata* and *Klieana levis* are to be found in all associations.

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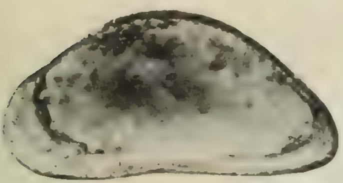
PLATE 1

Paracypris terraefullonica (Jones & Sherborn) p. 27

Fig. 1. Internal view, right valve. Io.2251. ×85.
Fig. 2. External view, left valve. Lectotype, I.1875. ×85.
Fig. 3. External view, right valve. I.1874. ×85.
Figs. 4–6. Right, dorsal and ventral views, complete carapace. Io.2250. ×85.

Darwinula incurva sp. nov. p. 28

Fig. 7. External view of crushed specimen, left side, showing muscle scars. Paratype, Io.2274. ×70.
Fig. 8. Muscle scars. Paratype, Io.2274. ×180.
Fig. 9. Internal view of left valve showing denticulate ventral margin. Paratype, Io.2261. ×70.
Figs. 10–12. Ventral, left and right views, complete carapace. Holotype, Io.2259. ×70.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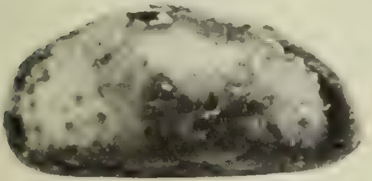
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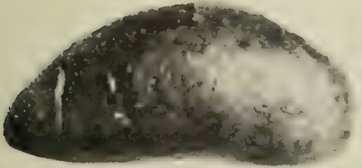
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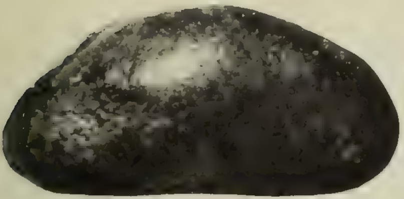
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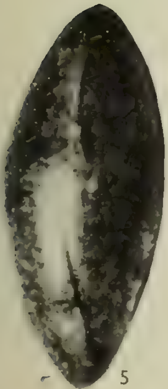
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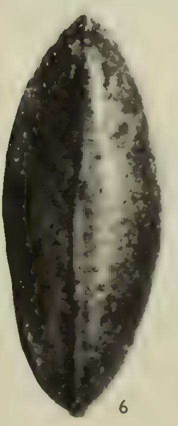
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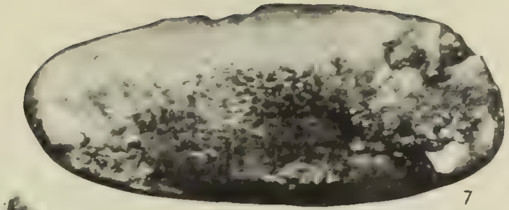
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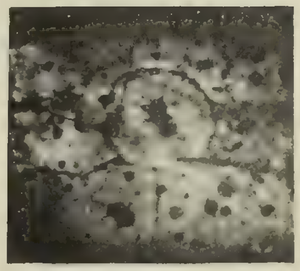
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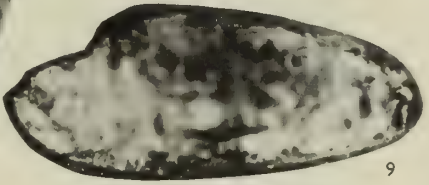
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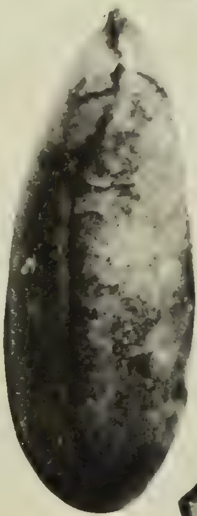
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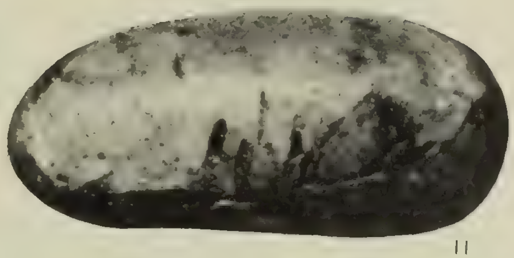
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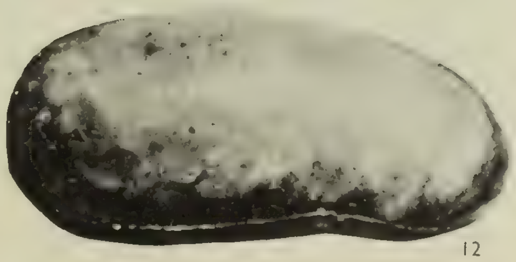
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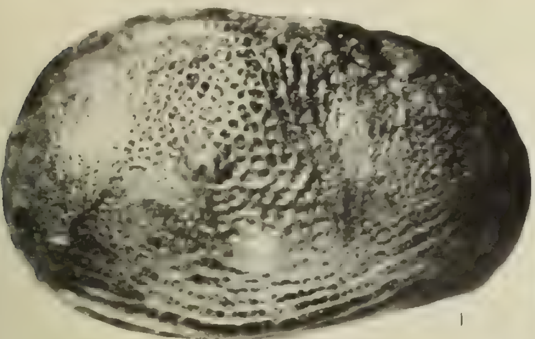
PLATE 2

Bisulcocypris anglica sp. nov. p. 30

Figs. 1–4. Right, left, ventral and dorsal views, male paratype. Io.2277. ×70.
Figs. 5–7. Dorsal, right and left views, female holotype. Io.2275. ×70.
Figs. 8–11. Left, right, dorsal and ventral views, juvenile paratype. Io.2280. ×70.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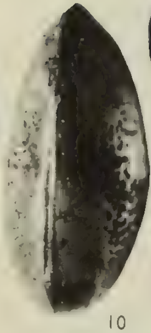
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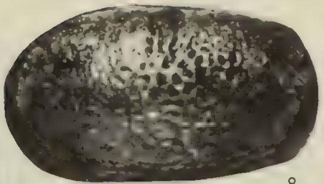
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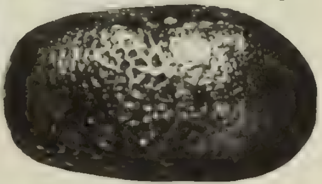
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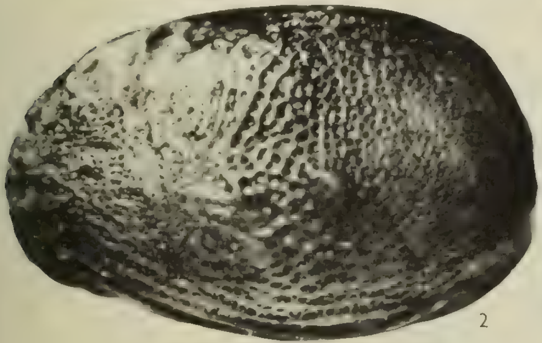
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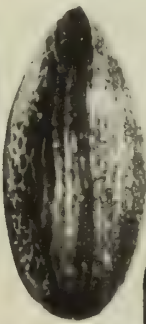
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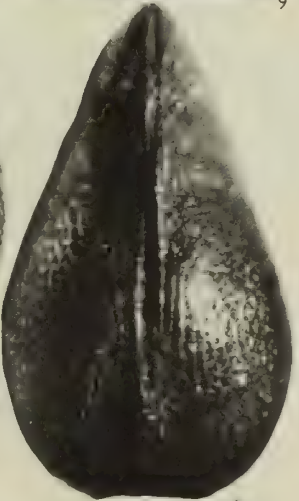
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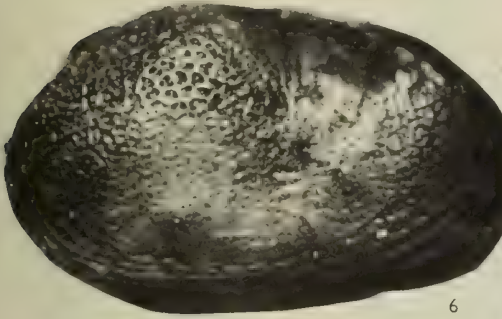
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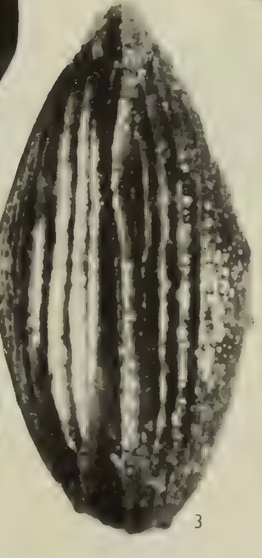
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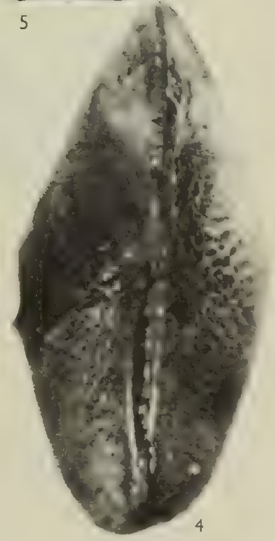
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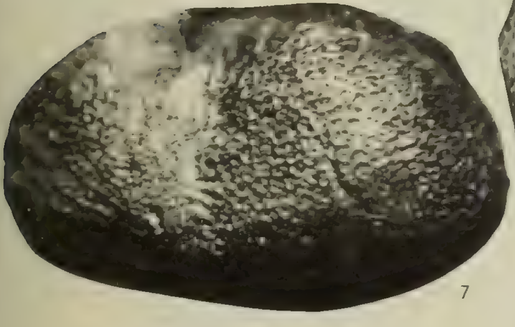
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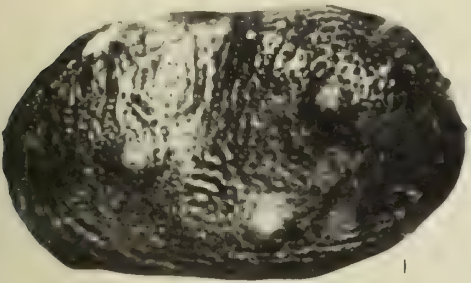
PLATE 3

Bisulcocypris ancasterensis sp. nov. p. 32

FIGS. 1–3. Left, right and dorsal views, female holotype. Io.2282. ×70.
FIGS. 4–6. Left, right and ventral views, male paratype. Io.2284. ×70.
FIGS. 7–10. Right, left, dorsal and ventral views, juvenile paratype. Io.2285. ×70.

Monoceratina scarboroughensis Bate p. 33

FIG. 11. Right view, female carapace. Io.2302. ×85.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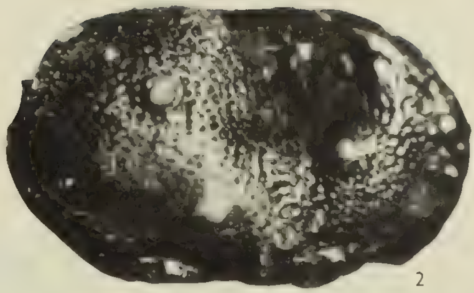
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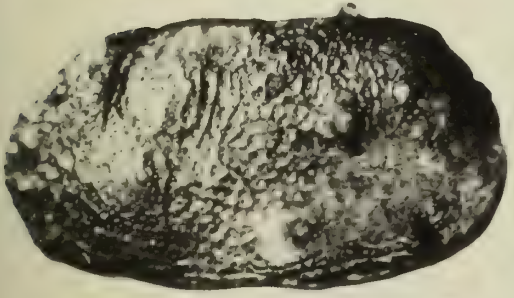
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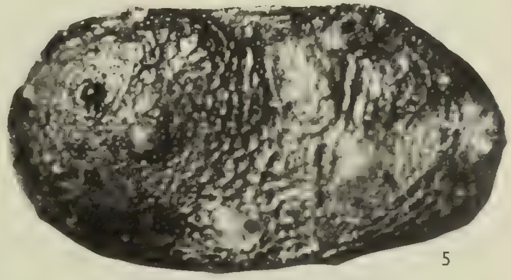
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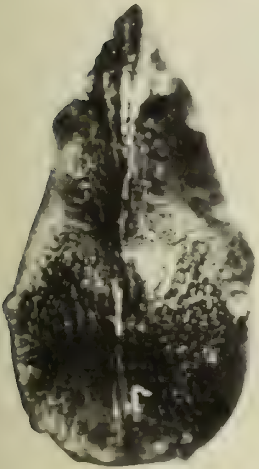
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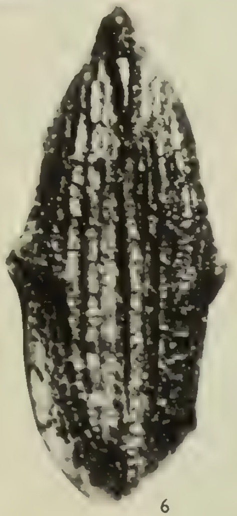
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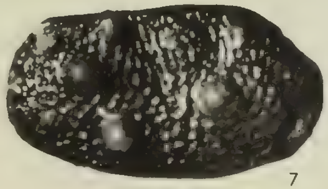
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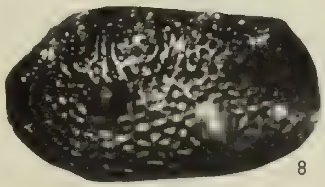
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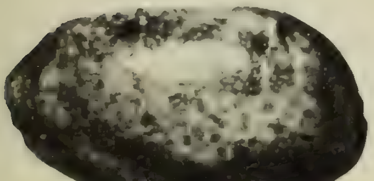
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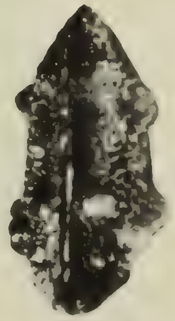
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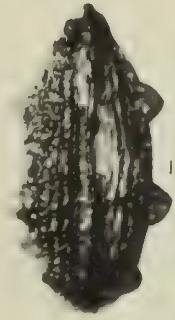
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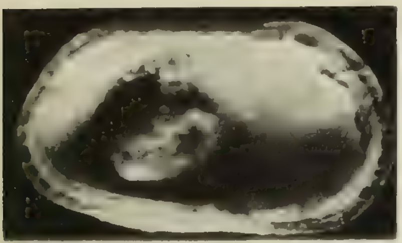
PLATE 4

Fabanella bathonica (Oertli) p. 33

FIG. 1. Internal view, female left valve to show radial pore canals. Io.2305. ×70.
FIGS. 2, 3. External and internal views, male right valve. Io.2303. ×70.
FIGS. 4, 5. Internal and external views, female left valve. Io.2304. ×70.

Galliaecytheridea*? *kingscliffensis sp. nov. p. 34

FIGS. 6, 7. Right and left views, female carapace. Holotype, Io.2316. ×80.
FIG. 8. Dorsal view of hinge, male left valve. Paratype, Io.2322. ×100.
FIG. 9. Internal view, female left valve. Paratype, Io.2321. ×80.
FIG. 10. Dorsal view showing median bar of hinge, female left valve. Paratype, Io.2321. ×100.
FIG. 11. Internal view, female right valve. Paratype, Io.2326. ×85.
FIG. 12. Muscle scars, female right valve. Paratype, Io.2326. ×250.



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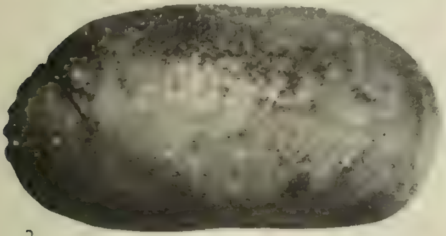

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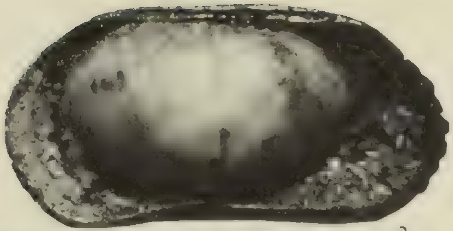

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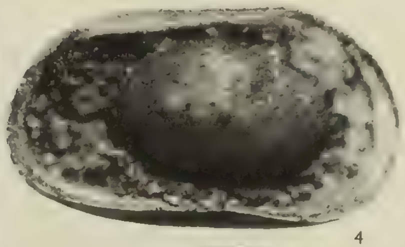

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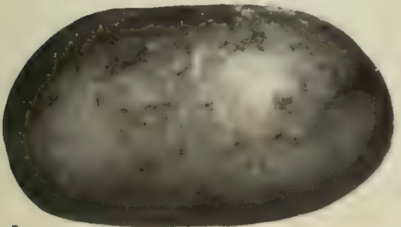

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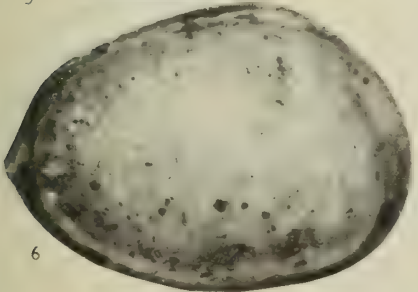

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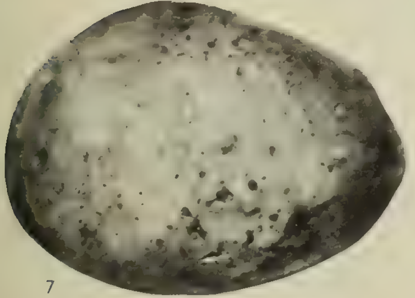

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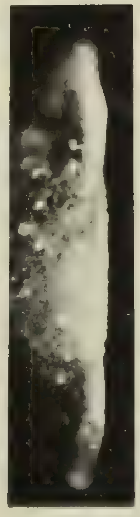

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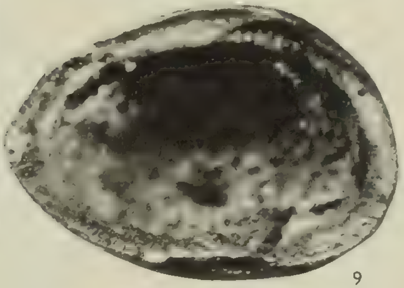

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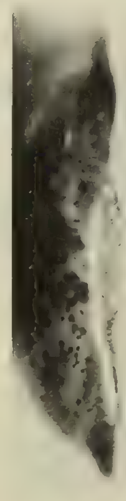

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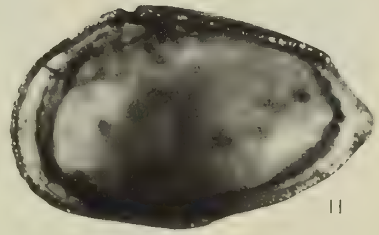

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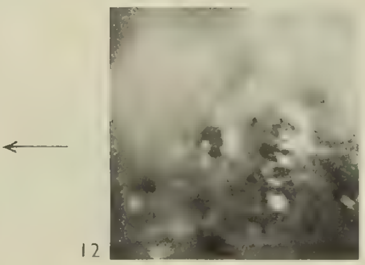

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PLATE 5

Galliaecytheridea*? *kingscliffensis sp. nov. p. 34

FIG. 1. Internal view to show radial pore canals, female left valve. Paratype, Io.2321. ×85.

FIGS. 2, 3. Dorsal and ventral views, female carapace. Holotype, Io.2316. ×80.

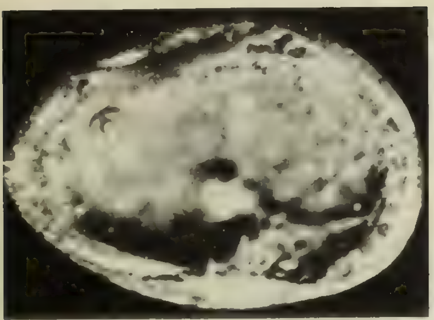
FIG. 4. External view, female left valve. Paratype, Io.2321. ×85.

FIGS. 5–8. Left, right, dorsal and ventral views, male carapace. Paratype, Io.2318. ×80.

Belekocytheridea punctata gen. et sp. nov. p. 36

FIGS. 9–12. Left, right, dorsal and ventral views female carapace. Holotype, Io.2328. ×85.

FIG. 13. Right side showing muscle scars, female carapace. Paratype, Io.2331. ×85.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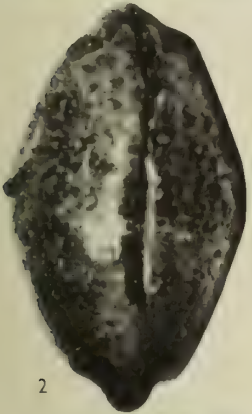
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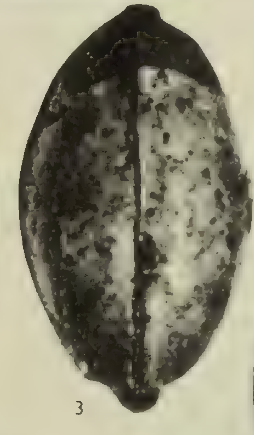
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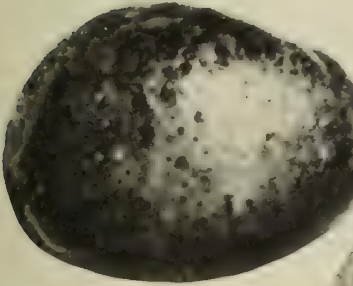
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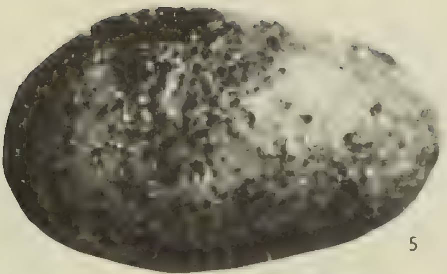
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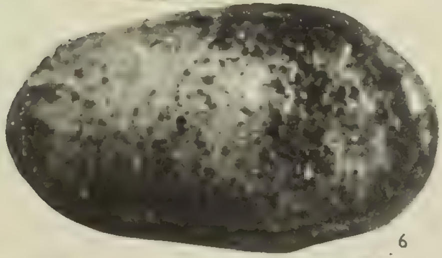
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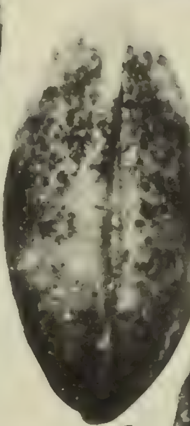
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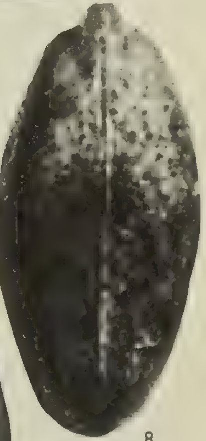
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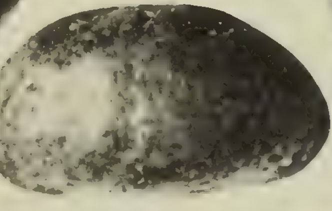
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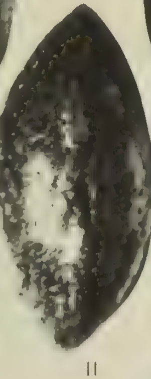
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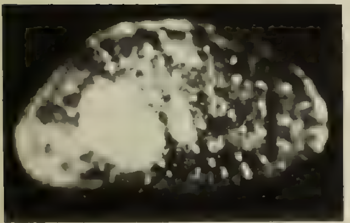
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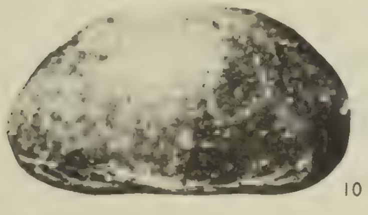
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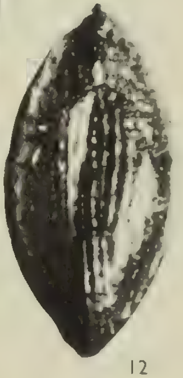
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PLATE 6

Belekocytheridea punctata gen. et sp. nov. p. 36

FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Paratype, Io.2329. ×85.

FIG. 5. Internal view, female left valve. Paratype, Io.2357. ×85.

Pichottia magnamuris sp. nov. p. 38

FIGS. 6–9. Left, right, dorsal and ventral views, female carapace. Holotype, Io.2358. ×85.

FIG. 10. Dorsal view to show median hinge bar, male left valve. Paratype, Io.2366. ×100.

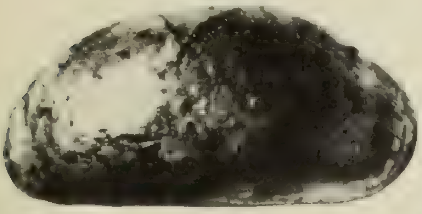
FIG. 11. Dorsal view of hinge, female left valve. Paratype, Io.2362. ×100.

FIG. 12. Dorsal view of hinge, female right valve. Paratype, Io.2363. ×100.

FIG. 13. Internal view to show radial pore canals, male right valve. Paratype, Io.2367. ×100.

FIG. 14. Muscle scars, male left valve. Paratype, Io.2368. ×180.

PLATE 6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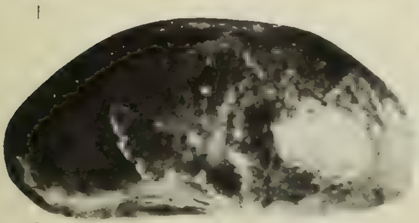
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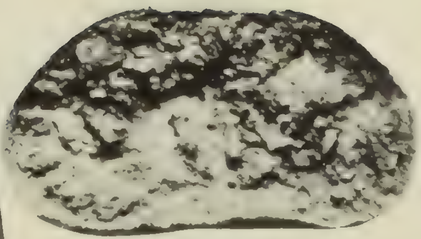
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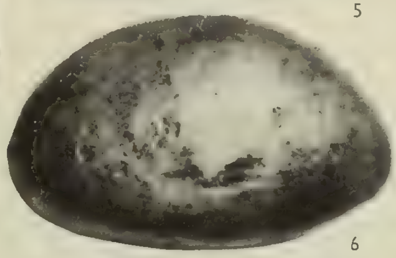
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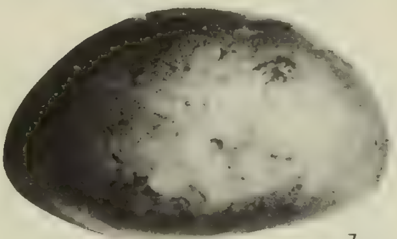
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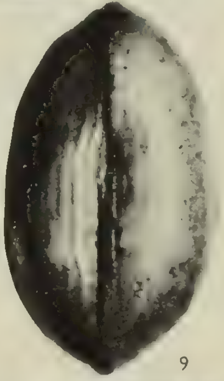
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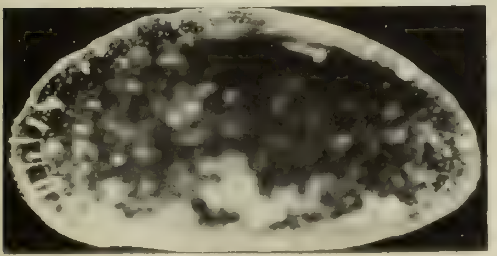
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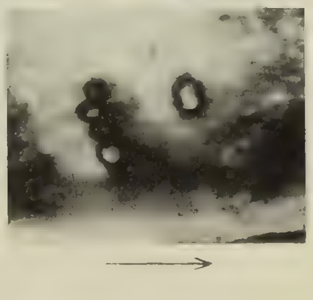
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PLATE 7

Pichottia magnamuris sp. nov. p. 38

FIGS. 1–4. Left, right, ventral and dorsal views, male carapace. Paratype, Io.2360. ×85.

FIG. 5. Internal view, female right valve. Paratype, Io.2363. ×85.

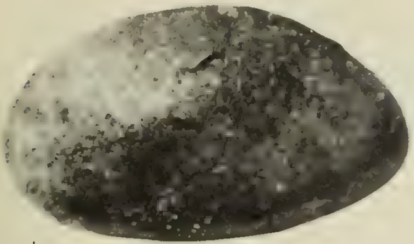
FIG. 6. Internal view, female left valve. Paratype, Io.2362. ×85.

Schuleridea (Eoschuleridea) bathonica subgen. et sp. nov. p. 41

FIGS. 7–10. Left, right, dorsal and ventral views, female carapace. Holotype, Io.2369. ×85.

FIG. 11. Dorsal view of hinge, female right valve. Paratype, Io.2376. ×100.

FIGS. 12, 13. Female right valve showing radial pore canals. Fig. 12 ×160, fig. 13 ×85. Paratype, Io.2373.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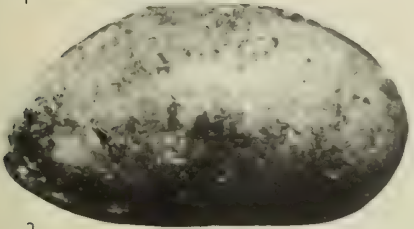
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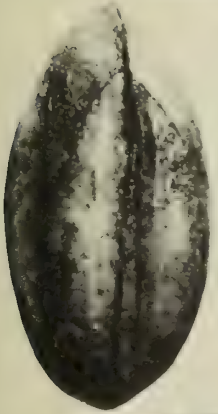
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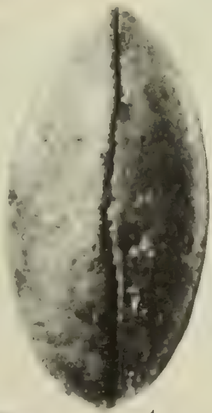
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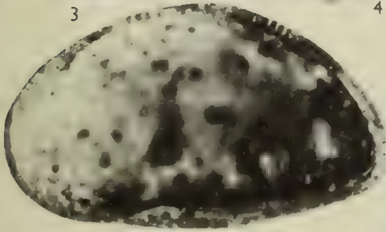
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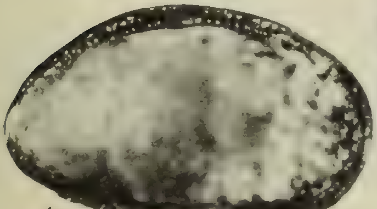
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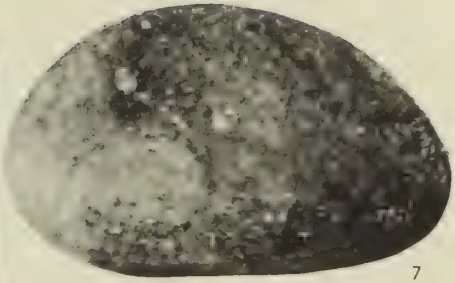
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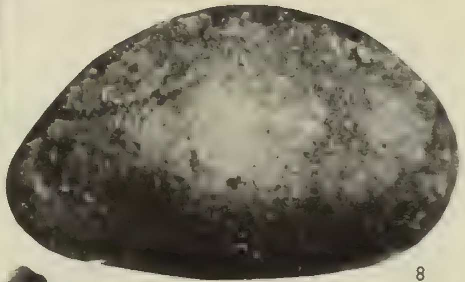
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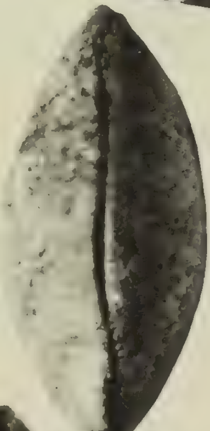
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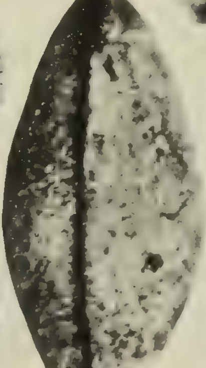
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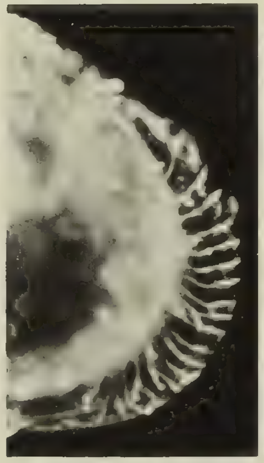
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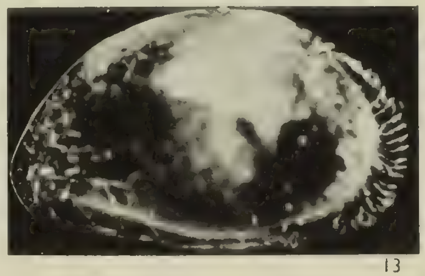
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PLATE 8

Schuleridea (Eoschuleridea) bathonica subgen. et sp. nov. p. 41

FIG. 1. Internal view to show hinge, female right valve. Paratype, Io. 2373. × 100.

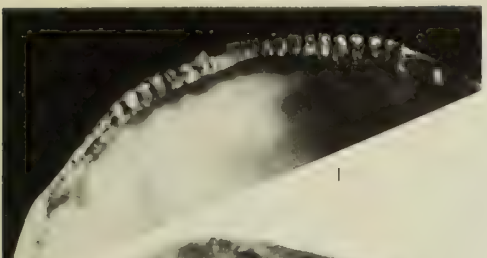
FIGS. 2, 3. External and internal views, male left valve. Paratype, Io. 2379. × 85.

FIGS. 4, 5. Internal and external views, female left valve. Paratype, Io. 2375. × 85.

FIGS. 6, 7. External and internal views, female right valve. Paratype, Io. 2376. × 85.

FIGS. 8–10. Dorsal, right and ventral views, male carapace. Paratype, Io. 2370. × 85.

FIG. 11. Muscle scars, note large size of antennal scar, male left valve. Paratype, Io. 2378. × 300.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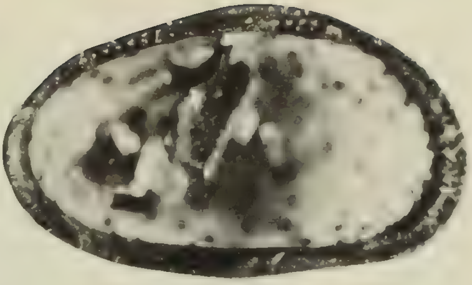
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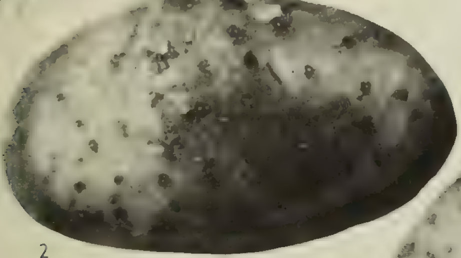
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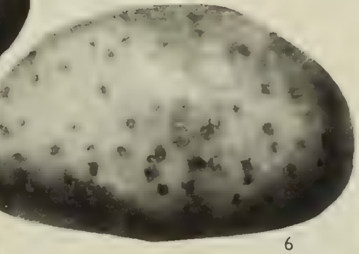
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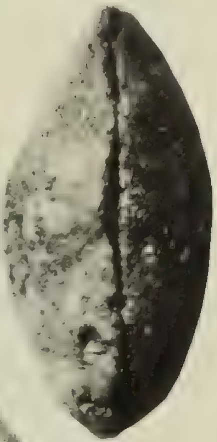
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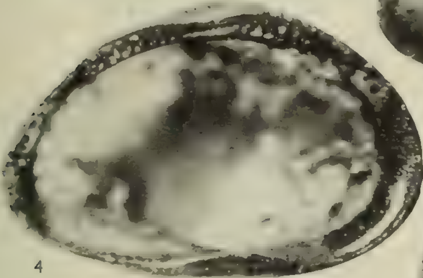
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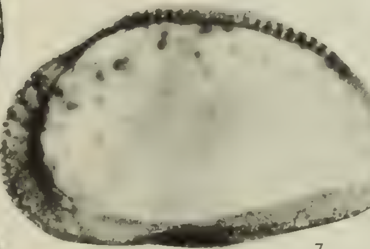
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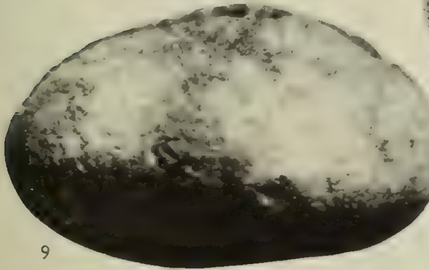
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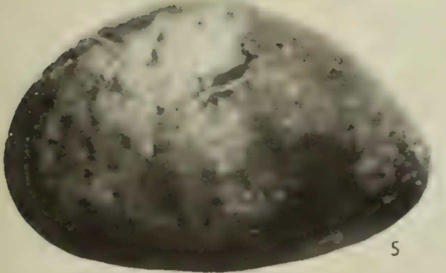
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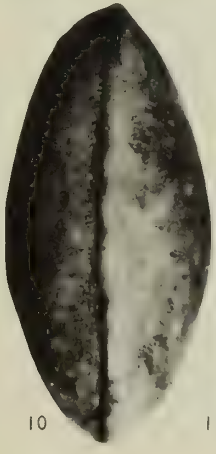
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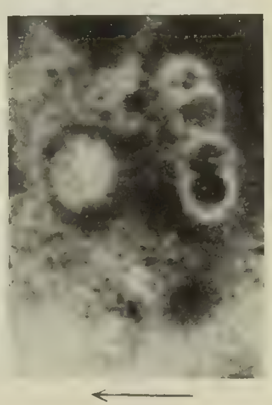
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PLATE 9

Praeschuleridea quadrata sp. nov. p. 42

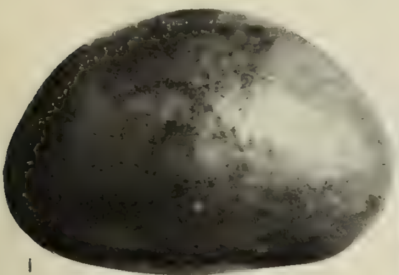
FIGS. 1–4. Right, left, dorsal and ventral views, female carapace. Holotype, Io.2395. ×85.

FIGS. 5–7. Dorsal view (×100), external and internal views, female right valve. Paratype, Io.2399. ×85.

FIGS. 8, 9. Internal views to show radial pore canals and hinge, female left valve. Paratype, Io.2398. ×85.

FIGS. 10, 11. Left and dorsal views, male carapace. Paratype, Io.2397. ×85.

FIG. 12. Muscle scars, male left valve. Paratype, Io.2400. ×300.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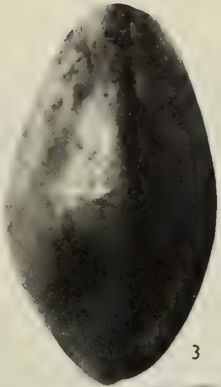
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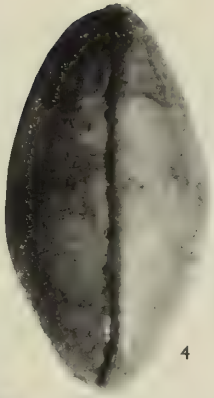
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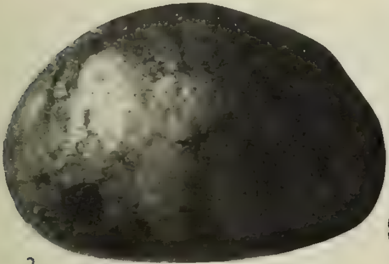
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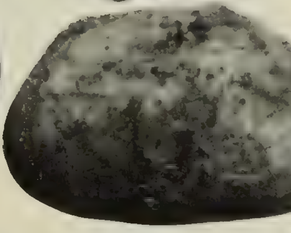
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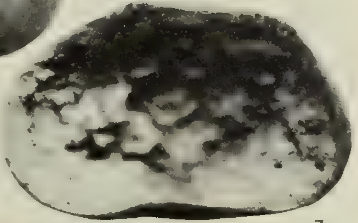
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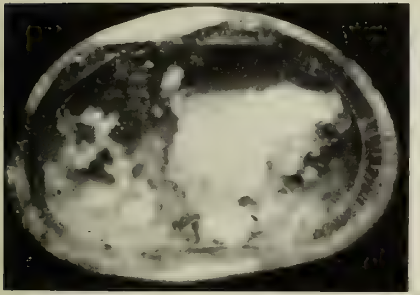
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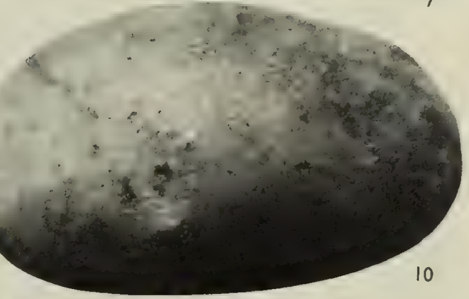
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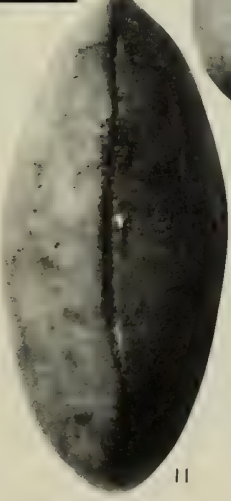
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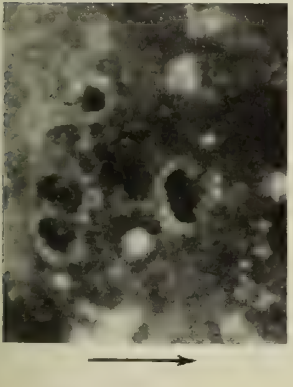
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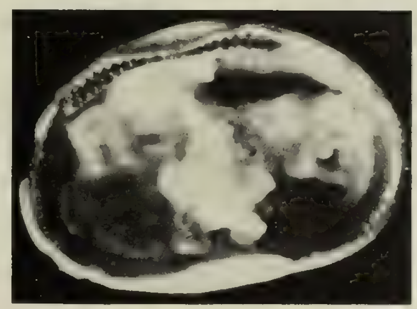
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PLATE 10

Metacytheropteron drupacea (Jones) p. 44

FIGS. 1, 2. External view and internal view showing radial pore canals, male left valve. Io.2415. ×85.

FIGS. 3, 4. Left and right views, female carapace. Jones' original specimen, holotype, IN.43498. ×85.

FIGS. 5, 7. External and internal views, female left valve. Io.2414. ×85.

FIGS. 6, 8, 9. Internal and external views, ×85, and dorsal view, ×100, male right valve. Io.2416.

Progonocythere levigata sp. nov. p. 45

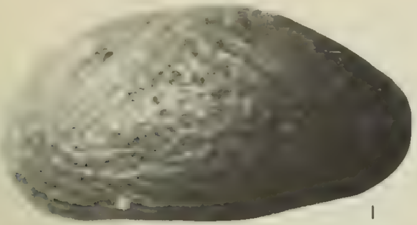
FIG. 10. Dorsal view of hinge to show terminal teeth and plate-like extension of the anterior portion of the median groove. Female right valve. Paratype, Io.2420. ×100.

FIGS. 11, 12. External and internal views, female left valve. Holotype, Io.2419. ×70.

FIG. 13. Muscle scars of holotype, Io.2419. ×170.

FIG. 14. Internal view, female right valve. Paratype, Io.2420. ×70.

PLATE 10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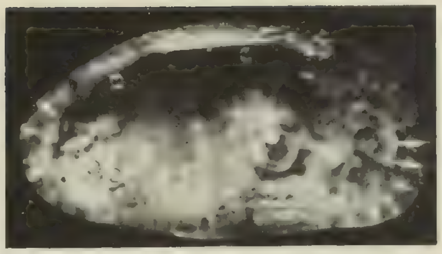
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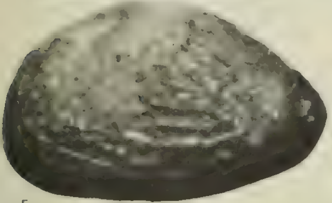
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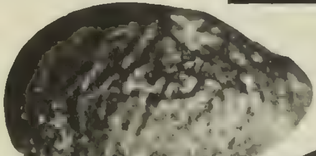
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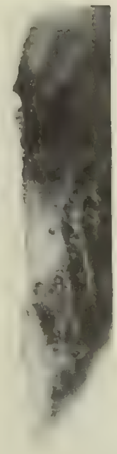
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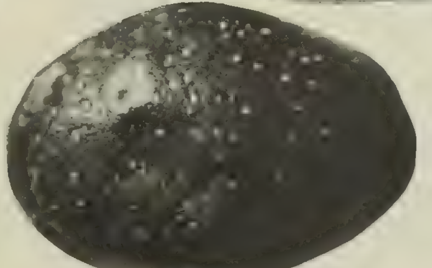
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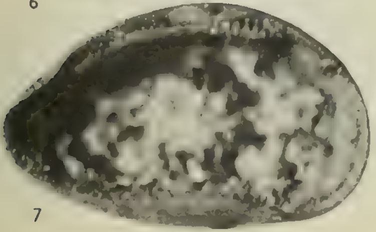
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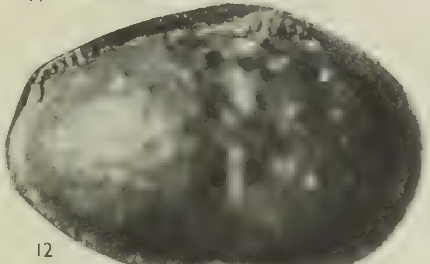
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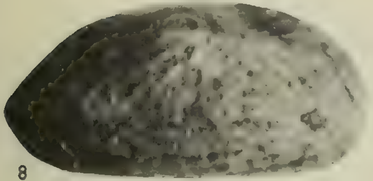
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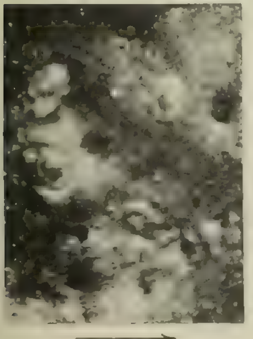
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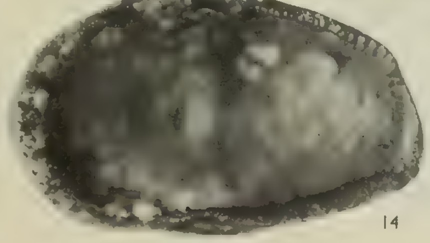
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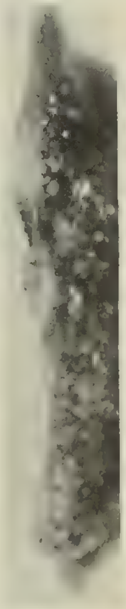
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PLATE 11

Progonocythere levigata sp. nov. p. 45

FIG. 1. Internal view, male right valve. Paratype, Io.2422. ×70.

FIGS. 2–4. External and internal views, ×70, and muscle scars, ×310, male left valve. Paratype, Io.2421.

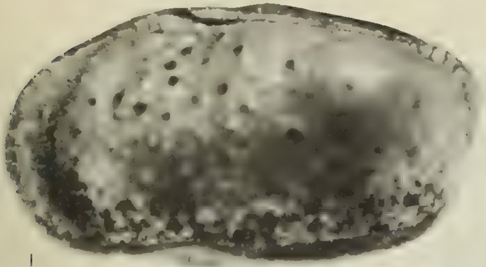
FIGS. 5–8. Dorsal, ventral, left and right views, female carapace. Paratype, Io.2423. ×70.

FIG. 9. External view, female right valve. Paratype, Io.2420. ×70.

Progonocythere rugosa sp. nov. p. 46

FIGS. 10–13. Right, left, dorsal and ventral views, female carapace. Holotype, Io.2434. ×70.

FIG. 14. Dorsal view, female right valve. Paratype, Io.2438. ×100.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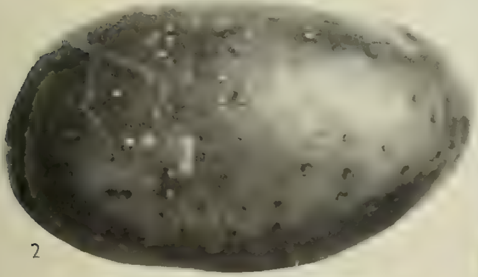
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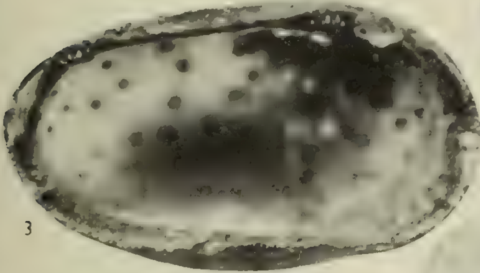
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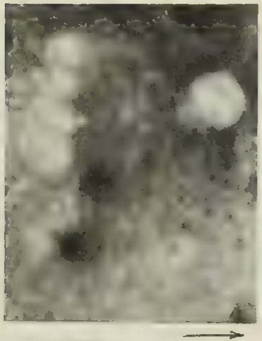
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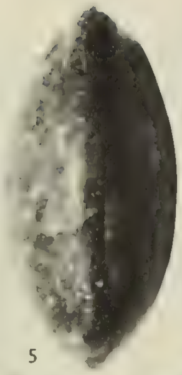
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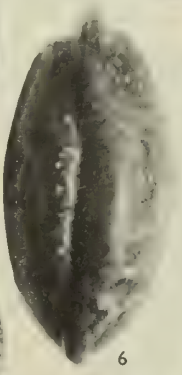
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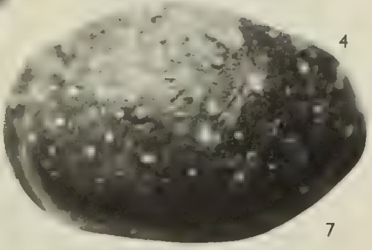
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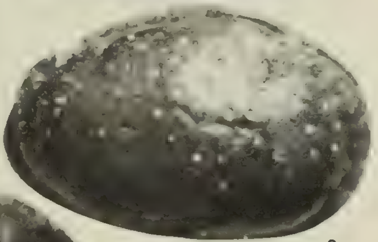
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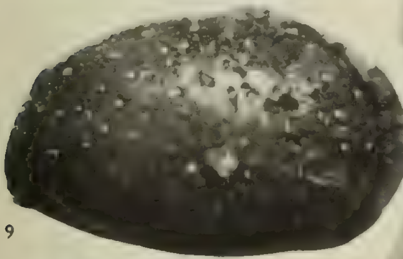
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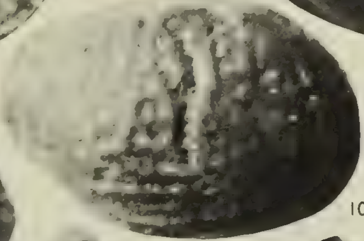
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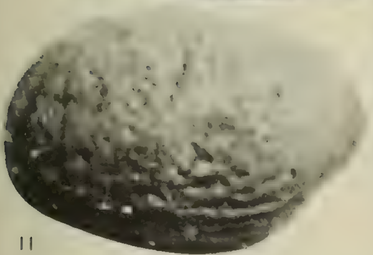
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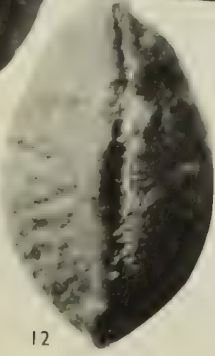
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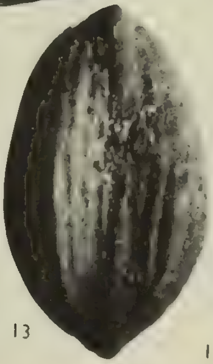
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PLATE 12

Progonocythere rugosa sp. nov. p. 46

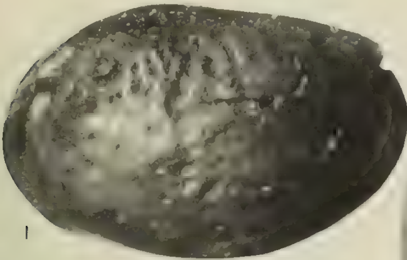
FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Paratype, Io.2435, ×70.

FIGS. 5, 7, 9. Internal views to show radial pore canals and hinge, ×70, and muscle scars, ×350, male left valve. Paratype, Io.2437. ×70.

FIGS. 6, 8. External and internal views, female right valve. Paratype, Io.2438. ×70.

Progonocythere triquetra sp. nov. p. 48

FIGS. 10–13. Left, right, dorsal and ventral views, female carapace. Holotype, Io.2453. ×70.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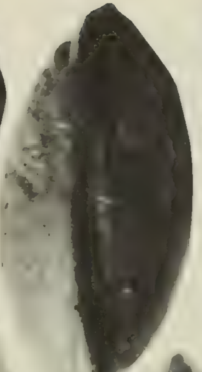
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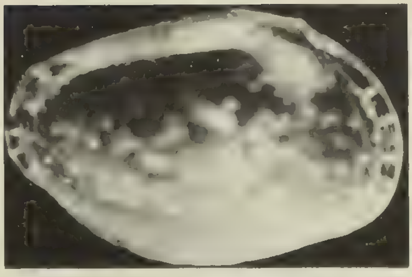
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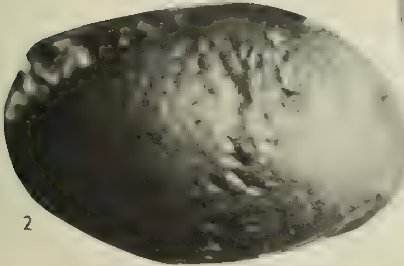
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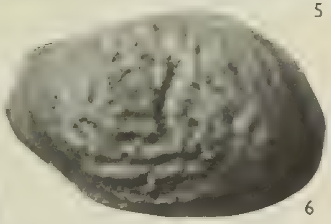
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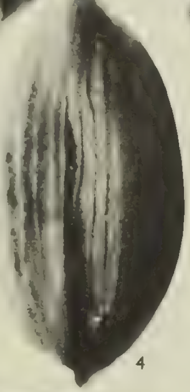
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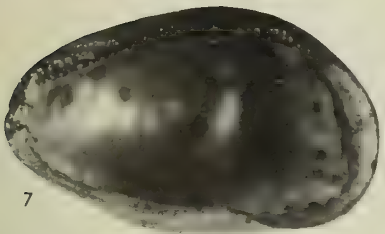
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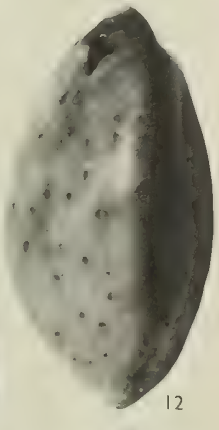
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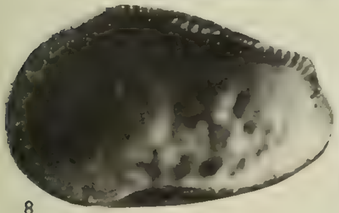
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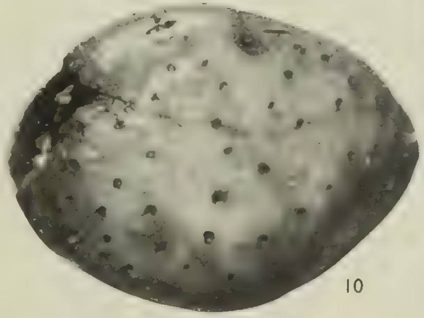
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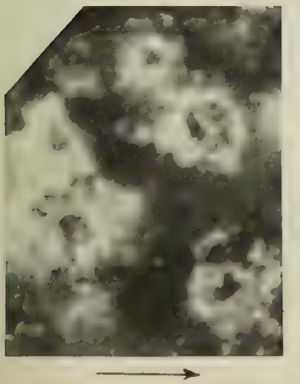
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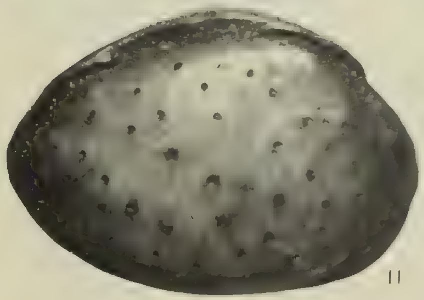
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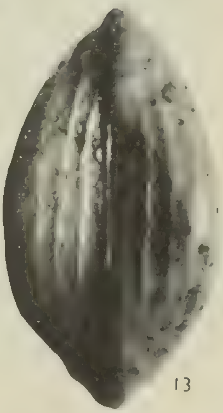
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PLATE 13

Progonocythere rugosa sp. nov. p. 46

FIG. 2. Dorsal view, hinge, male left valve. Paratype, Io.2437. ×100.

Progonocythere triquetra sp. nov. p. 48

FIGS. 1, 5, 6. Dorsal view, ×100, and external and internal views, ×70, male left valve. Paratype, Io.2456.

FIGS. 3, 9. Dorsal view, ×100, and external view, ×70, female left valve. Paratype, Io.2454.

FIGS. 4, 7, 8. Dorsal view, ×100, and external and internal views, ×70, female right valve. Paratype, Io.2455.

Glyptocythere guembeliana (Jones) p. 49

FIG. 10. External view, male right valve. Lectotype, IN.43493. ×70.

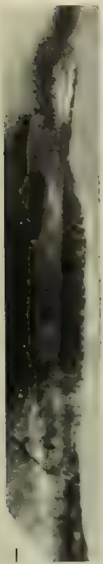
FIG. 11. External view, male right valve. Io.2466. ×70.

FIG. 12. External view, female right valve, Jones & Sherborn's. *Cytheridea pulvinar.* I. 1858 ×70.

FIG. 13. Dorsal view of median hinge bar, male left valve. Io.2465.

FIGS. 14, 16. External and internal views, female left valve. Io.2467. ×70.

FIG. 15. Internal view, female right valve. Io.2469. ×70.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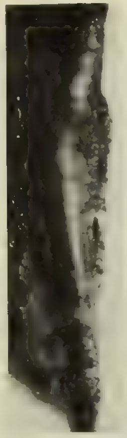
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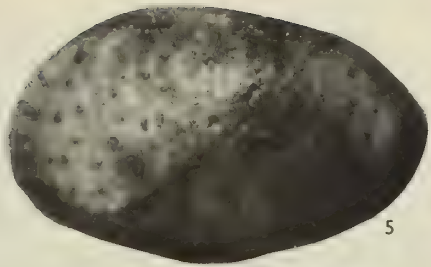
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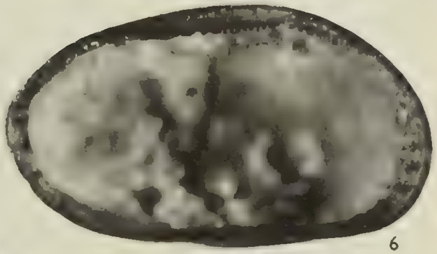
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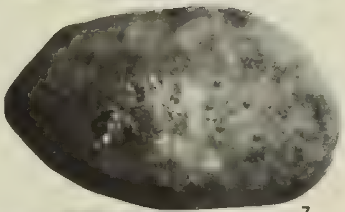
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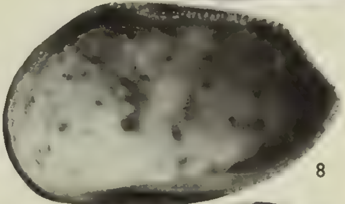
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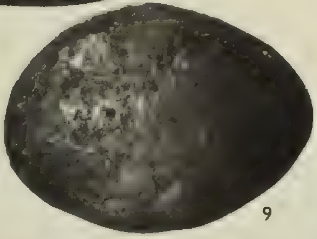
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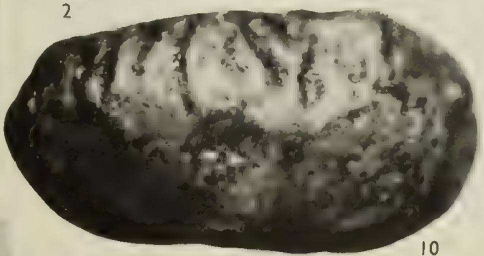
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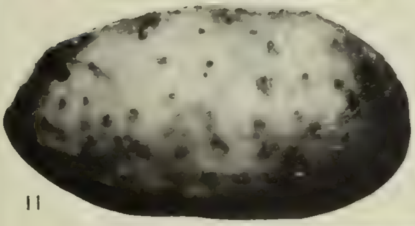
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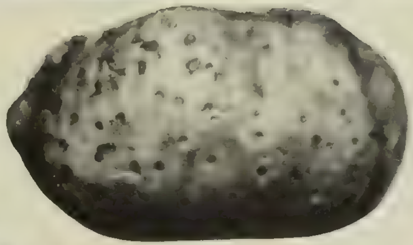
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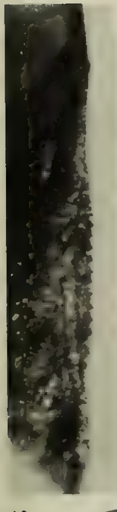
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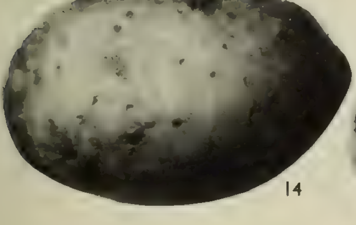
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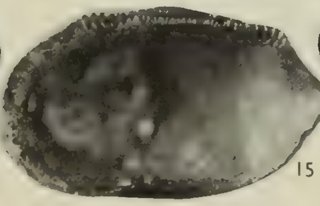
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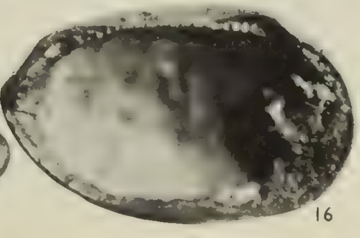
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PLATE 14

Glyptocythere guembeliana (Jones) p. 49

FIGS. 1, 5. External view showing ventral alate extension, and internal view, female right valve. Io.2472. ×70.

FIG. 2. External view of female right valve without alate extension. Io.2469. ×70.

FIGS. 3, 4. Dorsal and ventral views, female carapace. Io.2473. ×70.

FIGS. 6, 7. Internal view, female right valve showing radial pore canals. Fig. 6 ×150, fig. 7 ×70. Io.2468.

FIG. 8. Muscle scars ×360, female right valve. Io.2468.

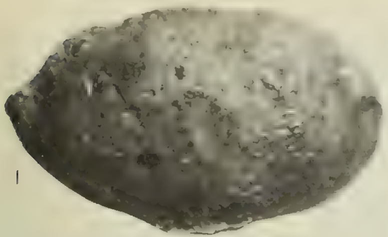
Glyptocythere juglandica (Jones) p. 51

FIG. 9. Right side, male carapace. Io.2516. ×70.

Klieana levis Oertli p. 51

FIGS. 10, 11, 13. Left, right and ventral views, male carapace. Io.2522. ×85.

FIG. 12. Internal view showing hinge, female left valve. Io.2521. ×85.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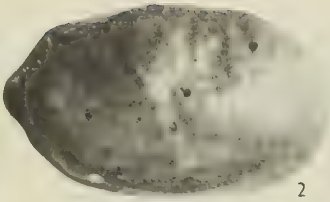
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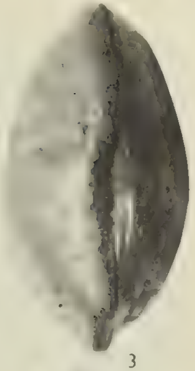
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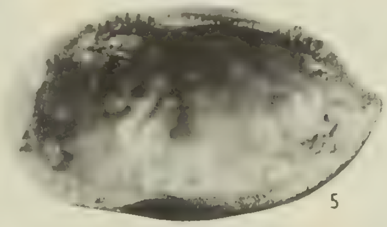
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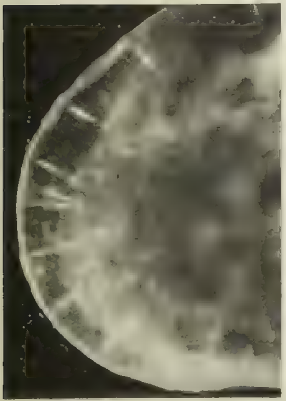
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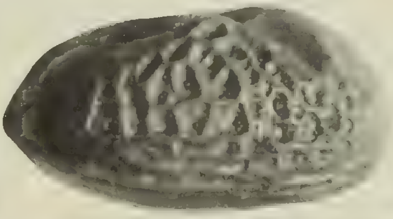
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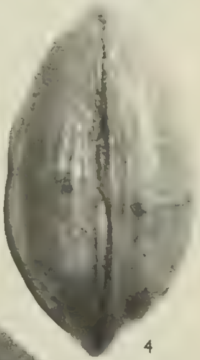
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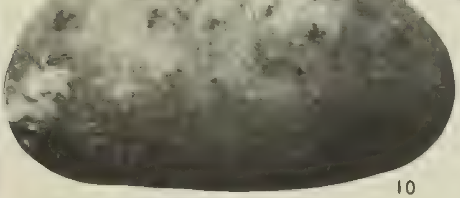
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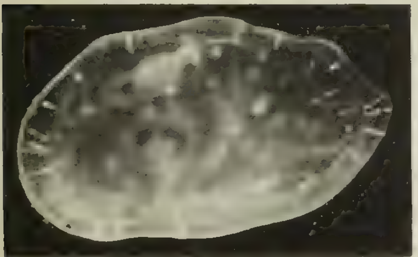
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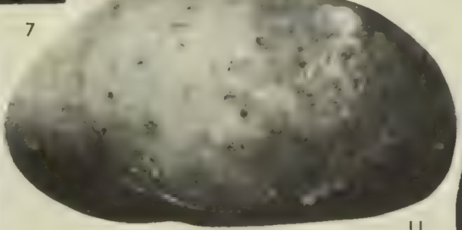
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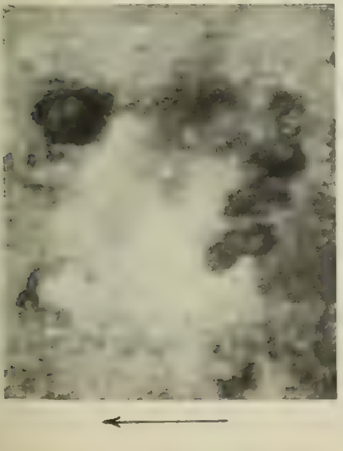
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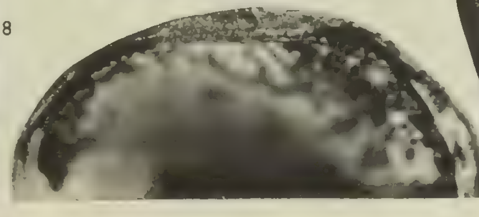
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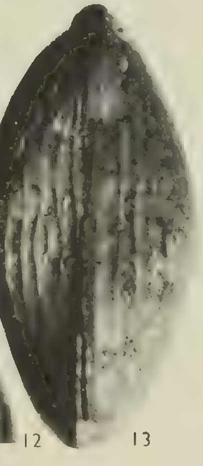
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PLATE 15

Klieana levis Oertli p. 51

FIG. 1. Internal view, female right valve, to show radial pore canals. Io.2520. ×85.

FIG. 2. Internal view, hinge, female right valve. Io.2520. ×100.

FIGS. 3, 4. Left and right views, female carapace. Io.2518. ×85.

FIG. 5. Muscle scars, female right valve. Io.2520. ×240.

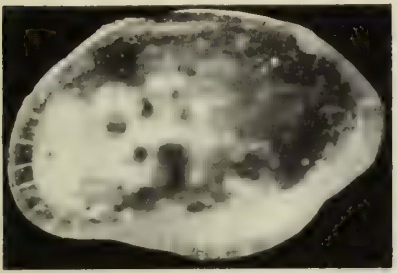
Lophocythere scabra scabra Triebel p. 52

FIG. 6. External view, female right valve. Io.2539. ×85.

Lophocythere septicostata sp. nov. p. 52

FIGS. 7–10. Left, right, dorsal and ventral views, female carapace. Holotype, Io.2542. ×85.

FIGS. 11–13. Internal and external views, ×85, and dorsal view, ×100, female right valve. Paratype I.1843. This specimen was originally figured by Jones & Sherborn 1888 as *Cytheridea bradiana* (Jones).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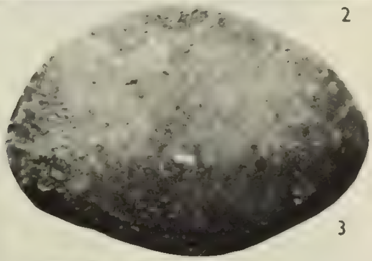
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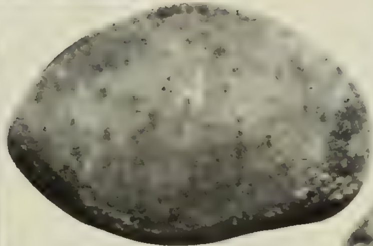
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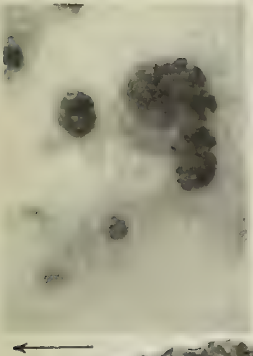
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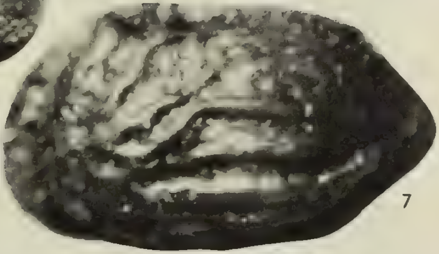
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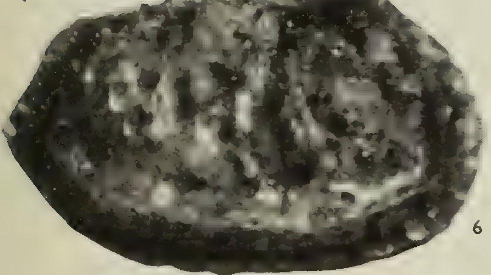
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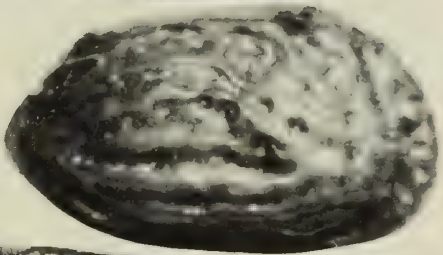
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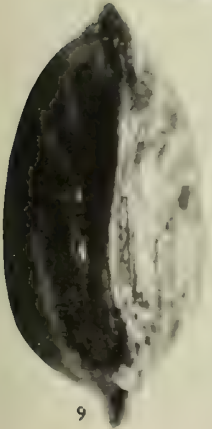
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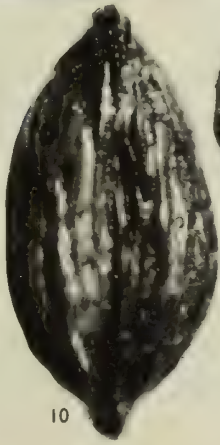
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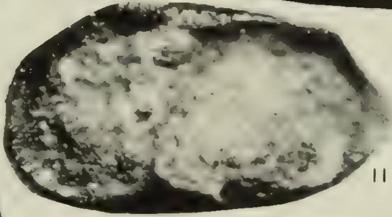
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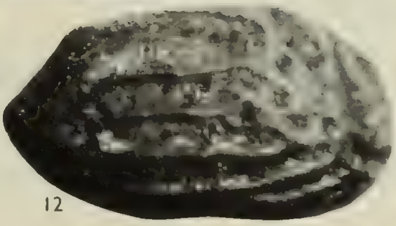
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PLATE 16

Lophocythere septicostata sp. nov. p. 52

FIGS. 1–4. Left, right, dorsal and ventral views, male carapace. Paratype, Io.2547. ×85.

Lophocythere transversiplicata sp. nov. p. 53

FIGS. 5–7. Left, right and dorsal views, male carapace. Paratype, Io.2626. ×85.

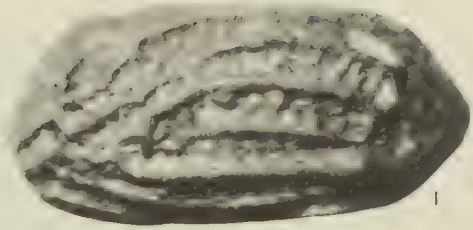
FIGS. 8–10. Left, dorsal and ventral views, female carapace. Holotype, Io.2625. ×85.

FIGS. 11, 12. Internal view, ×85, and dorsal view, ×100, female right valve. Paratype, Io.2627.

FIG. 13. External view, male right valve. Paratype, Io.2628. ×85.

FIG. 14. External view, male left valve. Paratype, Io.2629. ×85.

FIG. 15. Internal view showing radial pore canals, female right valve. Paratype, Io.2627. ×85.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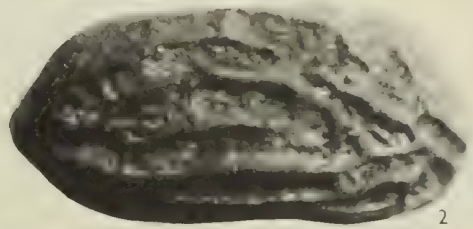
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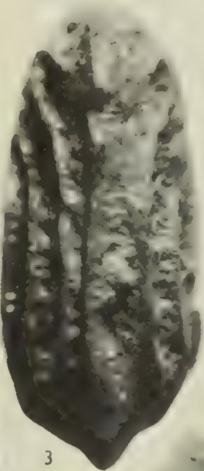
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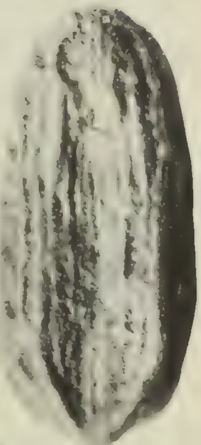
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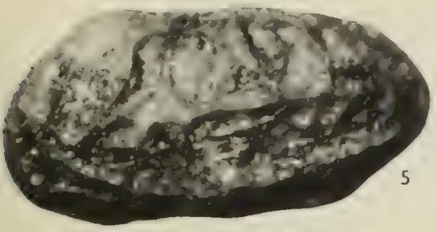
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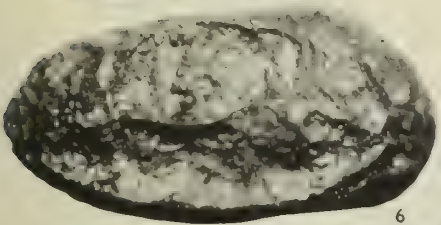
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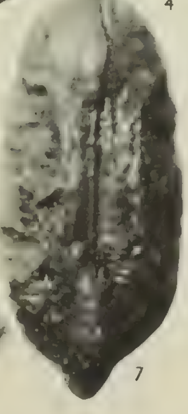
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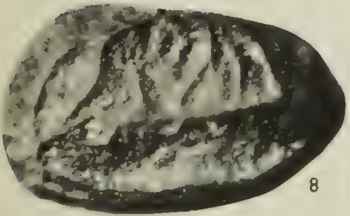
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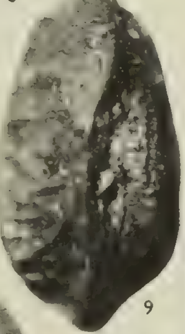
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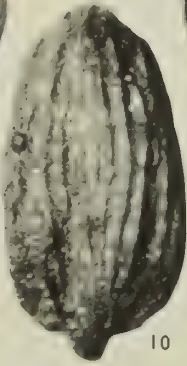
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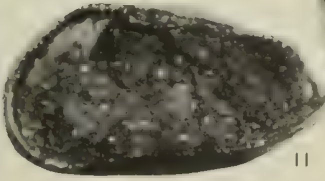
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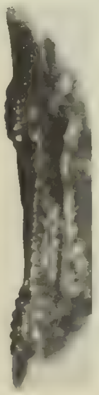
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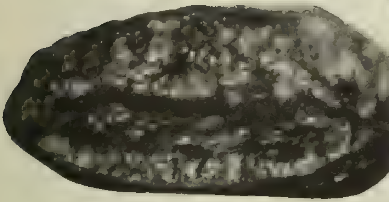
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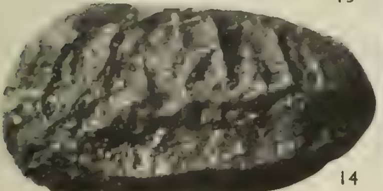
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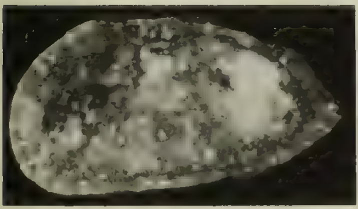
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PLATE 17

Macrodentina* (*Mediodentina*) *bathonica subgen. et sp. nov. p. 55

FIGS. 1–3. Left, right and ventral views, female carapace. Holotype, Io.2550. ×70.

FIGS. 4, 7, 12. External view (×70), internal and dorsal views of hinge (×100), female right valve. Note plate-like extension of the lower margin of the anterior part of the median groove in dorsal view. Paratype, Io.2556.

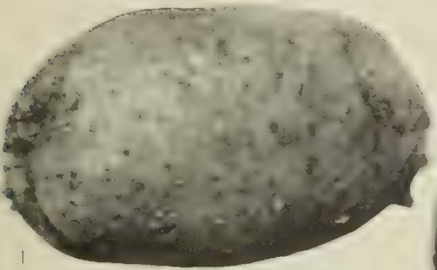
FIGS. 5, 6. External and internal views, female left valve. Paratype, Io.2554. ×70.

FIG. 8. Internal view showing radial pore canals, female right valve. Paratype, Io.2557. ×70.

FIG. 9. Internal view showing radial pore canals, male left valve. Paratype, Io.2552. ×70.

FIG. 10. Dorsal view showing median hinge bar, male left valve. Paratype, Io.2552. ×100.

FIG. 11. Dorsal view showing enlarged antero-median part of median bar, female left valve. Paratype, Io.2555. ×100.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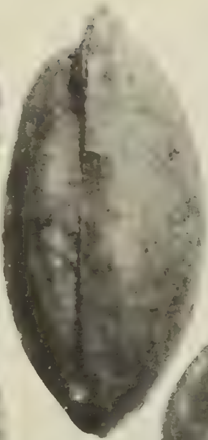
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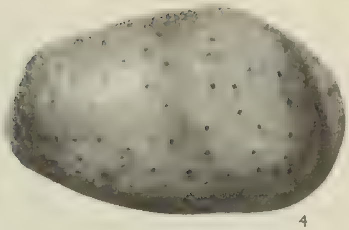
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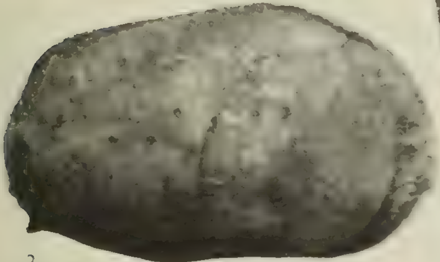
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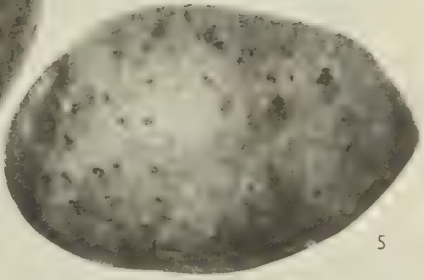
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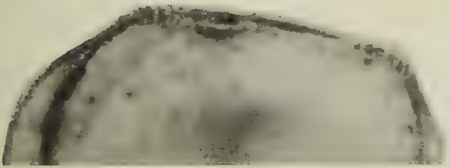
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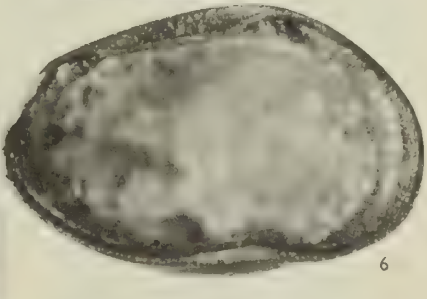
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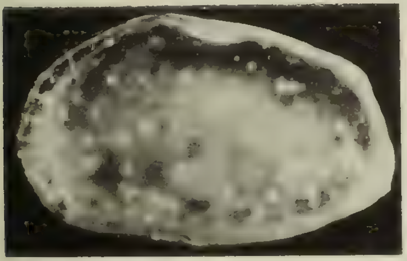
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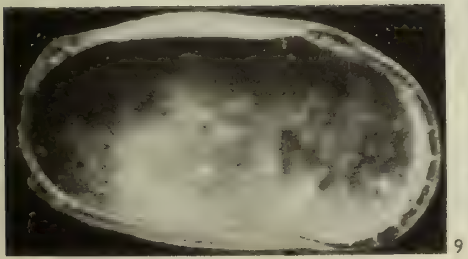
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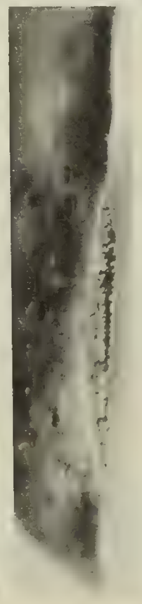
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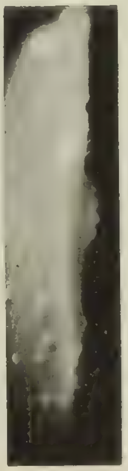
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PLATE 18

Macrodentina* (*Mediodentina*) *bathonica subgen. et sp. nov. p. 55

FIGS. 1, 4. External and internal views, male left valve. Paratype, Io.2552. ×70.

FIG. 2. External view to show strength of surface ornamentation in this specimen, masking the normal pore canals. Male left valve. Paratype, Io.2553. ×70.

FIG. 3. Muscle scars, female right valve. The dark ringed circles, including that showing a diagonal cross-bar, are normal pore canals. The mandibular scar is not shown in this illustration. Paratype, Io.2557. ×250.

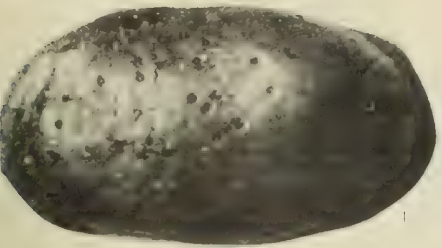
Marslatourella bullata sp. nov. p. 56

FIGS. 5–8. Right, left, dorsal and ventral views, male carapace. Paratype, Io 2575 ×70.

FIGS. 9–12. Right, left, dorsal and ventral views, female carapace. Paratype, Io.2579. ×70.

FIG. 13. External view, female right valve. Holotype, Io.2573. ×70.

FIG. 14. Internal view of hinge, female left valve. Paratype, Io.2578. ×100.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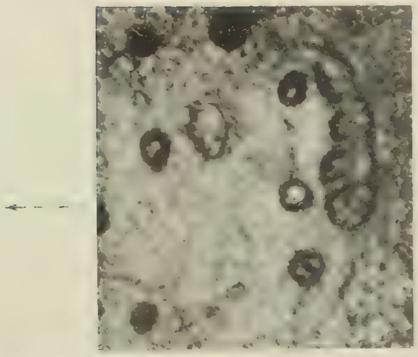
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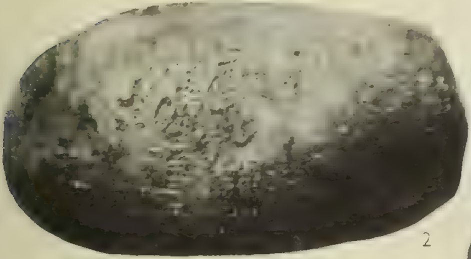
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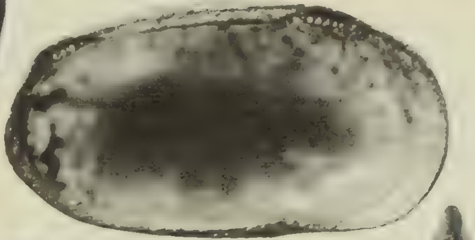
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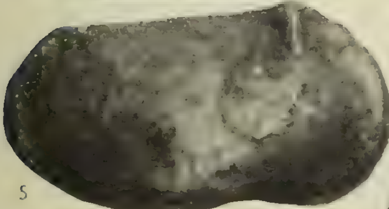
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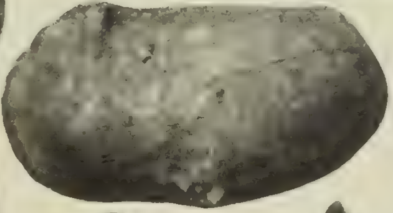
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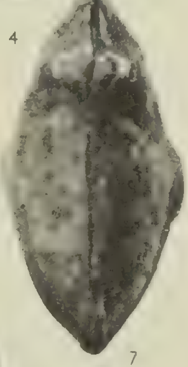
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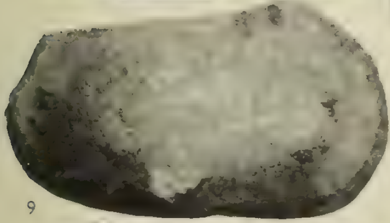
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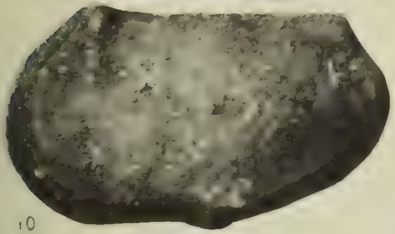
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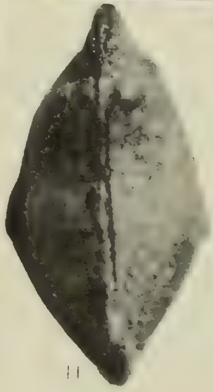
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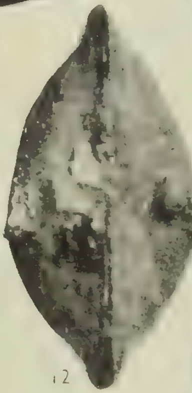
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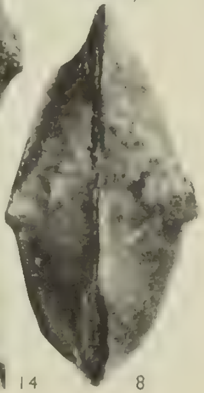
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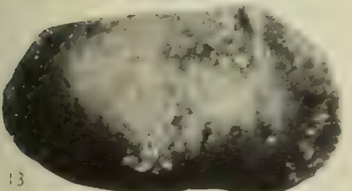
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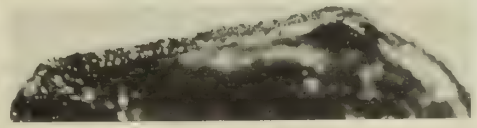
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PLATE 19

Marslatourella bullata sp. nov. p. 56

Figs. 1, 2. Internal view showing radial pore canals and external view. Female left valve. Paratype, Io.2578. ×70.

Micropneumatocythere postrotunda sp. nov. p. 57

Figs. 3–6. Left, right, dorsal and ventral views of carapace. Holotype, Io.2582. ×85.

Figs. 7, 8, 13. Internal and external views (×85) and dorsal view (×100), left valve. Paratype, Io.2584.

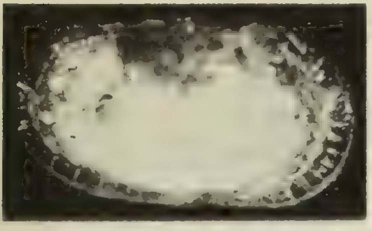
Figs. 9, 10, 14. External and internal views (×85) and dorsal view (×100), right valve. Paratype, Io.2586.

Fig. 15. Anterior radial pore canals, left valve. Paratype, Io.2585. ×160.

Fig. 16. Muscle scars, paratype, Io.2583. ×270.

Micropneumatocythere quadrata sp. nov. p. 58

Figs. 11, 12. External and internal views, female left valve. Paratype, Io.2595. ×85.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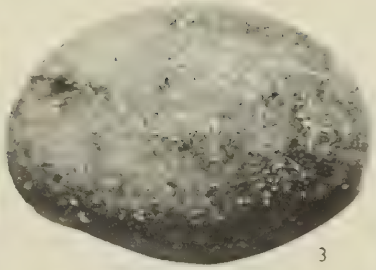
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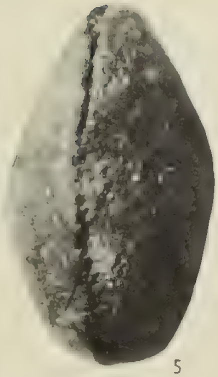
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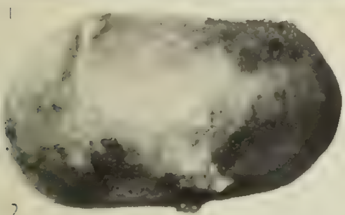
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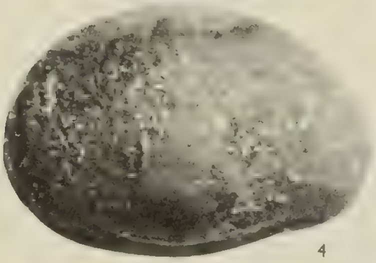
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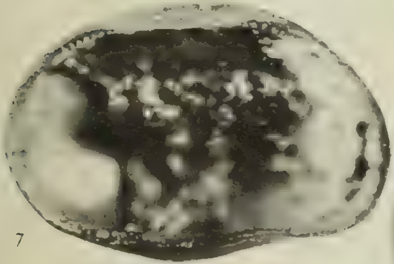
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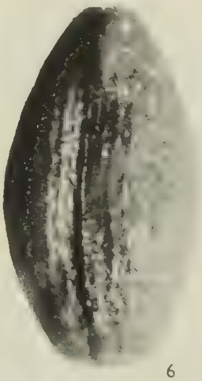
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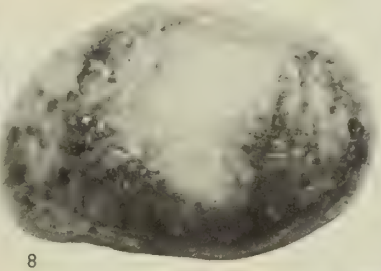
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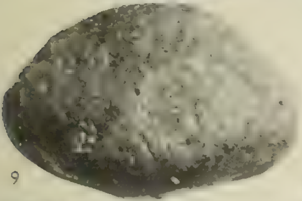
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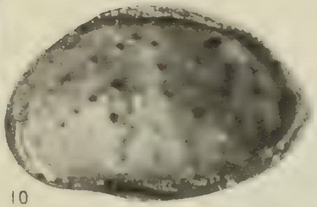
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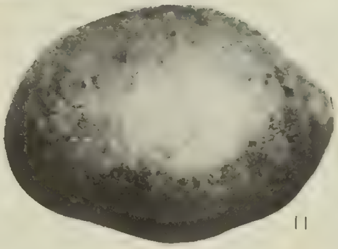
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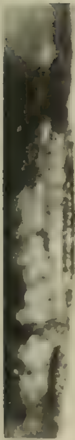
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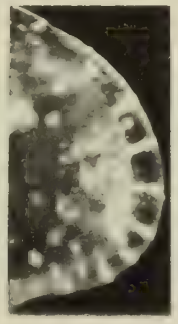
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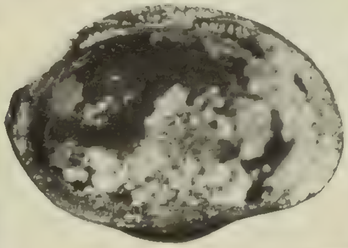
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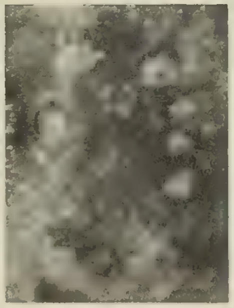
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PLATE 20

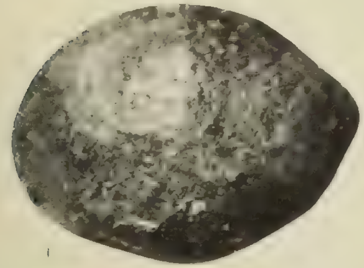
Micropneumatocythere quadrata sp. nov. p. 58

FIGS. 1–4. Left, right, dorsal and ventral views, female carapace. Holotype, Io.2592. ×85.

FIGS. 5–8. Left, dorsal, right and ventral views, male carapace. Paratype, Io.2593. ×85.

FIGS. 9, 10, 12. Internal and external views, ×85, dorsal view, ×100, female right valve. Paratype, Io.2594.

FIG. 11. Dorsal view, female left valve. Paratype, Io.2595. ×100.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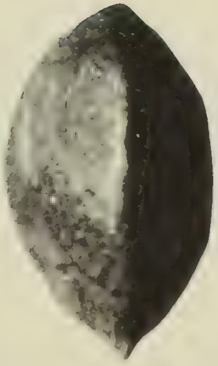
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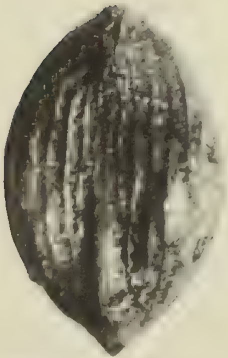
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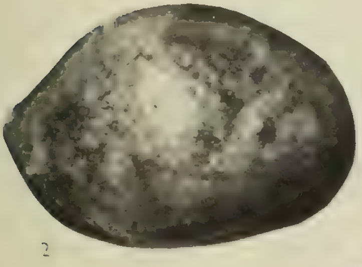
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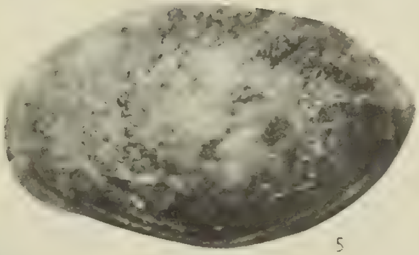
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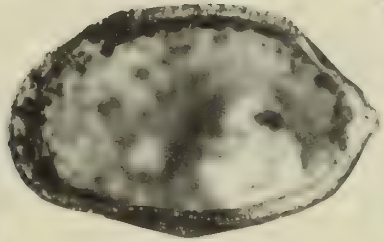
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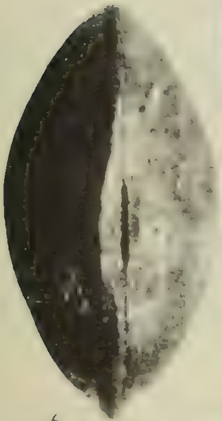
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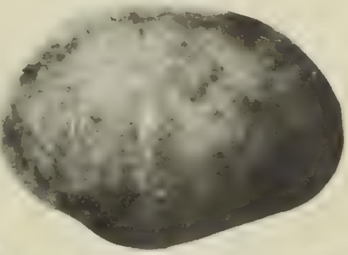
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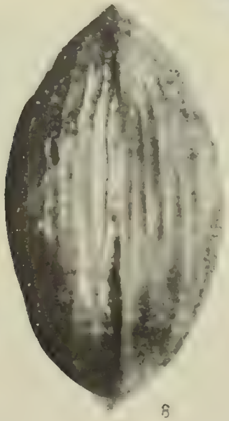
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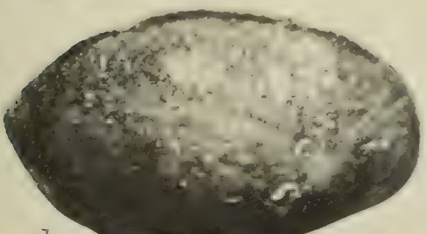
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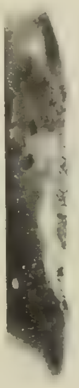
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PLATE 21

Micropneumatocythere subconcentrica (Jones) p. 60

FIGS. 1–4. Right, left, dorsal and ventral views, carapace. Io.2607. ×85.

FIGS. 5, 13. Dorsal view, ×100, and internal view to show radial pore canals, ×85. Left valve. Io.2608.

FIGS. 6, 11. Dorsal view, ×100, and external view, ×85, right valve. Io.2609.

FIGS. 7, 8. External and internal views, left valve. Lectotype, IN.43505. ×85.

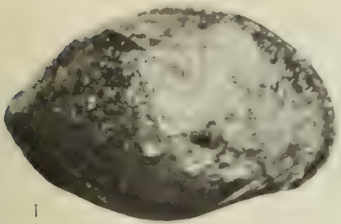
FIGS. 9, 10. External and internal views, left valve. Io.2610. ×85.

FIG. 12. Muscle scars, left valve. Io.2608. ×340.

Oligocythereis fullonica (Jones & Sherborn) p. 61

FIG. 14. External view, left valve. Io.2624. ×85.

FIG. 15. External view, right valve. Io.2623. ×85.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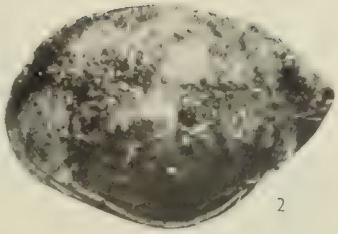
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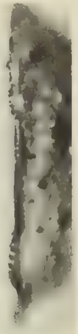
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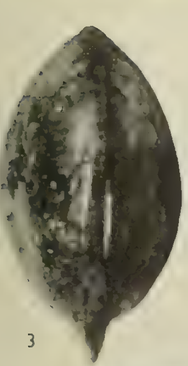
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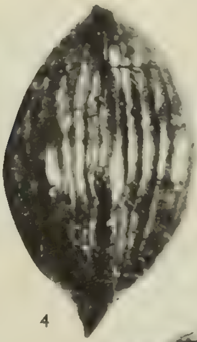
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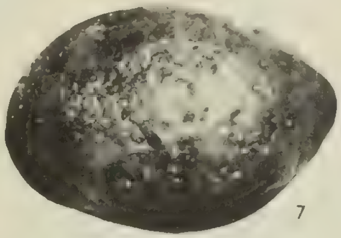
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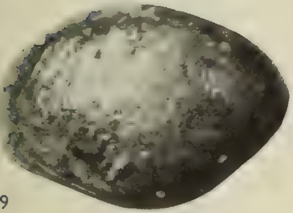
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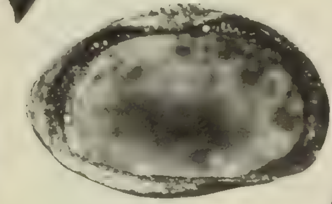
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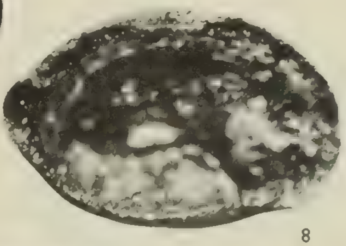
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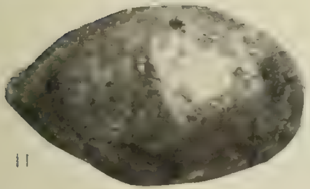
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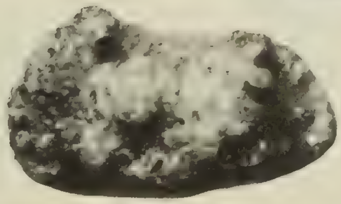
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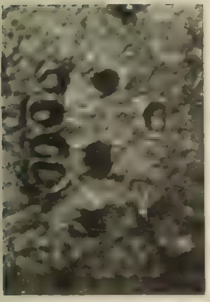
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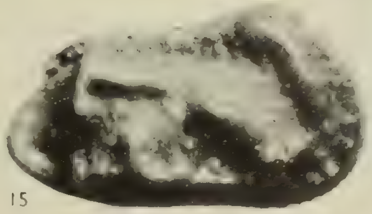
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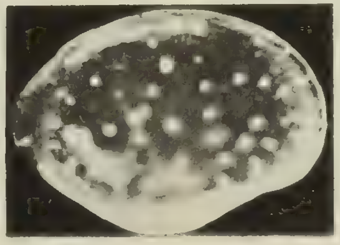


PLATE 22

Platycythere verriculata gen. et sp. nov. p. 62

FIGS. 1–4. Right, left, dorsal and ventral views, male carapace. Holotype, Io.2613. ×85.

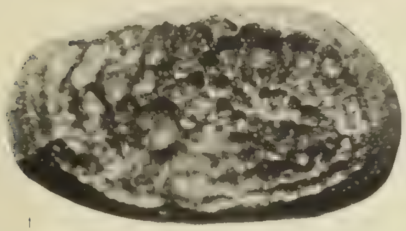
FIGS. 5–8. Right, left, ventral and dorsal views, female carapace. Paratype, Io.2621. ×85.

FIG. 9. Internal view, male right valve. Paratype, Io.2615, ×85.

FIG. 10. Dorsal view showing enlarged anterior portion of median hinge bar. Male left valve. Paratype, Io.2616. ×100.

FIG. 11. Left side of juvenile carapace. Paratype, Io.2622, ×85.

FIGS. 12, 13. Muscle scars, ×220, anterior radial pore canals, ×200, male right valve. Paratype, Io.2614.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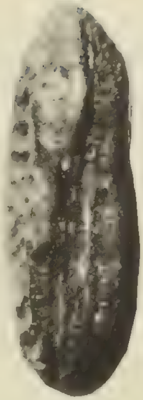
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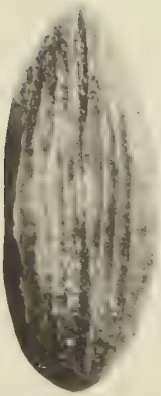
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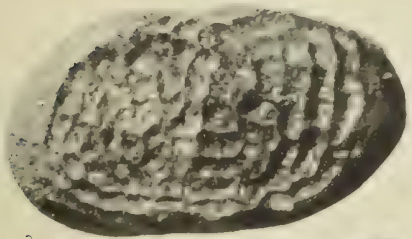
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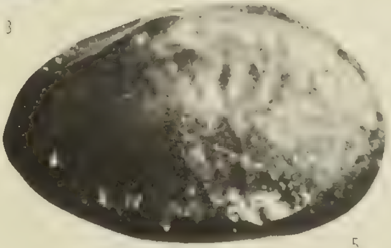
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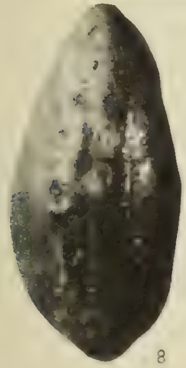
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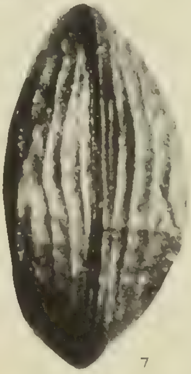
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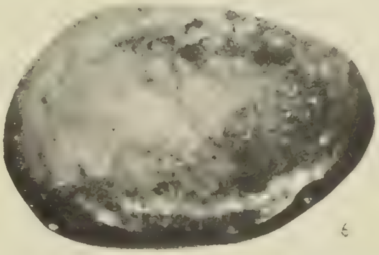
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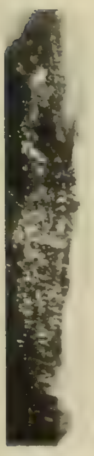
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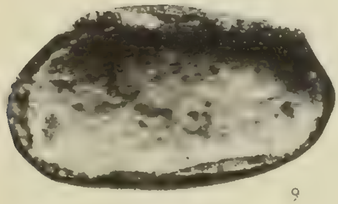
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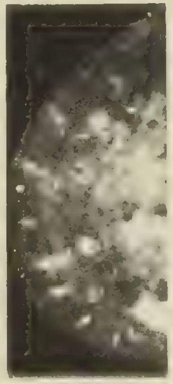
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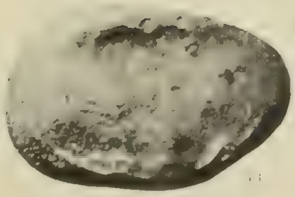
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NATURAL HIST

NEW CRETACEOUS BERYCOID FISHES FROM THE LEBANON

C. PATTERSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 14 No. 3
LONDON: 1967

3 APR 1967
NATURAL HISTORY

NEW CRETACEOUS BERYCOID FISHES FROM THE LEBANON

BY

COLIN PATTERSON, Ph.D.

Pp. 67–109 ; 4 *Plates* ; 11 *Text-figures*

BULLETIN OF
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NEW CRETACEOUS BERYCOID FISHES FROM THE LEBANON

By COLIN PATTERSON

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SYNOPSIS

This paper contains descriptions of four berycoids, three from the Cenomanian fish beds of Hakel and Hajula, *Lissoberyx* gen. nov. *dayi* (Smith Woodward) (Trachichthyidae), *Stichocentrus liratus* gen. et sp. nov. and *Caproberyx pharsus* sp. nov. (both Holocentridae), and one from the Upper Senonian beds of Sahel Alma, *Gnathoberyx stigmosus* gen. et sp. nov. (Trachichthyidae). *Lissoberyx dayi* is the most primitive berycoid yet known, and lies near the origin of the suborder. *Acrogaster anceps* Arambourg is probably a second species of *Lissoberyx*. *Gnathoberyx* is the only acanthopterygian yet discovered in which a toothed maxilla is the dominant bone in the upper jaw. A new subfamily Caproberycinae is made for the Cretaceous Holocentridae, which do not appear to be ancestral to the Tertiary and living subfamilies. These and other points are considered in a discussion of the origin and early evolution of the Berycoidei. Preliminary observations on the fish beds at Hakel suggest that they were deposited in a submarine canyon or gully, the abundance of fishes being due to mass mortalities caused by " waterbloom ". It is suggested that the fish beds at Hakel and Hajula are of Middle Cenomanian age rather than Upper Cenomanian.

I. INTRODUCTION

IN the spring of 1964 I spent a month in the Lebanon, collecting Upper Cretaceous fishes and examining the very large collection of these fishes in the Geology Department of the American University, Beirut. This paper is the first of a series dealing with new material resulting from this trip. It contains preliminary discussions of the palaeoecology and age of the Cenomanian fish beds of the Lebanon, and descriptions of four berycoid fishes, three of them representing new genera.

It is a pleasure to acknowledge here all the help I received in the Lebanon, in particular from Prof. Theodore Raven, Geology Department, American University,

Beirut, who gave me every facility and allowed me to borrow specimens from the collection in his care. My thanks are also due to Mrs. Raven, to Mr. Bud Young of the Geology Department and Dr. Karl George of the Zoology Department in the American University, and especially to my friends Mr. & Mrs. I. N. H. Seymour of Beirut. I am also most grateful to Dr. D. D. Bayliss for his comments on the microfauna of the Lebanon fish beds, to Mr. C. I. Macadie for his help in preparing the specimens, and to Mr. N. Tanti, who photographed the fishes.

The material described here is in the collections of the British Museum (Natural History), identified by the prefix " P." before the registered number, and the Geology Department of the American University, Beirut, referred to by " AUB " before the number.

II. LOCALITIES AND CONDITIONS OF DEPOSITION

The fishes described here are from the three classic fish localities in the Lebanon, Hakel, Hajula (both Cenomanian in age) and Sahel Alma (Upper Senonian). I was unable to visit Sahel Alma and have nothing to add to published information on the locality (Roger, 1946 ; Dubertret, 1963 : 119 ; Patterson, 1964 : 365 and references cited there). At Hakel and Hajula, two villages about 4 km. apart, at about 700 m., respectively 11 and 9 km. inland from Byblos (Jebail), the fish beds are very similar in age and fauna (Roger, 1946 ; Dubertret, 1963 : 57 ; Patterson, 1964 : 362 and references cited there). Although much has been published on the fauna of Hakel and Hajula, knowledge of the conditions under which the beds were deposited rests on Roger's monograph (1946) which dealt with the invertebrates of all three localities and gave particular attention to the palaeoecology. Roger had not visited the Lebanon and described the fauna of Hakel as being from two localities, Hakel and Maifouk (a neighbouring village), when only one exposure of fish beds exists there (Dubertret, 1963 : 58). Roger concluded (p. 83) that the Cenomanian fish beds were laid down as soft, fine mud on a deoxygenated bottom in channels between shallows supporting reefs of rudists, well clear of coasts. He visualized the rocks as being deposited in several hundred metres of water, basing this estimate on the crustacean fauna and the similarity of the rocks to *Globigerina* ooze.

Further fieldwork is necessary before a detailed account of the palaeoecology of the Cenomanian fish beds can be given, but some preliminary observations are worth mentioning here. At Hajula the exposure is in the centre of the village and building, cultivation and the inhabitants prevented me from forming an accurate estimate of the extent and thickness of the fish beds, but at Hakel the beds are well exposed in a narrow valley, in dip on the southern side and in strike on the northern, the beds dipping to the north at about 30°. The exposure is about 250 m. long (east–west) and about 200 m. broad (north–south). On the south side of the valley blasting was carried out in the centre of the exposure about six years ago. The fish beds are at least 20 m. thick and their base has not been seen : above they pass into flaggy, unfossiliferous limestones. The fish beds consist of thin-bedded, siliceous limestones alternating irregularly with more massive limestones. Occasional nodules and lenses of impure chert occur throughout the beds. The rock is normally pale buff in colour, but bluish and grey beds occur occasionally, the former mainly in the massive limestones, the latter in the thin-bedded. Under the hammer the rock often gives off a bituminous smell, as Roger (1946 : 76) noted. From museum collections one gains the impression that the bedding planes are flat and smooth, but in fact there is a great deal of complex small scale folding in the thinner beds, probably due to slumping in the unconsolidated sediment. This suggests that the fish beds were deposited on a slope. Apart from these contorted beds, the bedding planes are flat and I have seen no ripple marks nor any signs of current bedding or graded bedding.

At each end of the exposure the fish beds terminate abruptly against massive, structureless and unfossiliferous limestones. These junctions are not faulted as earlier authors have thought, for higher in the valley wall beds pass across the line of junction without interruption. At the junction the fish beds are slightly contorted and shattered, tending to bend upwards, but there is no sign of any breccia or conglomerate. The line of junction is steeply inclined outwards (away from the centre of the exposure) at both ends of the fish beds, but where the junction is best exposed, in the stream bed at the eastern end of the exposure, the fish beds appear to undercut the massive limestone. Two possible explanations of this contact present themselves : the first that the massive limestones are a reef, evidently entirely recrystallized since no fossils or structures are preserved ; the second that the limestones are the walls of a submarine canyon or gully. The following points, each of which is difficult to reconcile with deposition close to a reef (indicating shallow, well oxygenated water), suggest that the second of these interpretations is preferable :

(i) the high organic content and bituminous smell of the fish beds, together with the complete absence of sessile benthos, indicating a deoxygenated bottom.

(ii) the absence of any reef breccia at the contact between the massive limestones and the fish beds.

(iii) the microfauna of the fish beds consists of abundant radiolarians, moderately abundant pelagic Foraminifera (*Hedbergella*) and rare benthonic Foraminifera (textulariids) : my colleague Dr. D. D. Bayliss, who kindly examined thin sections of the fish beds and identified the Foraminifera, considers the rock to be a foraminiferan/radiolarian ooze, suggesting near bathyal depths.

As a preliminary hypothesis, it is therefore suggested that the Cenomanian fish beds of Hakel were laid down in a submarine canyon or gully which in some way served as a trap for fishes and invertebrates which were preserved in large numbers because of the deoxygenated bottom and a supply of fine sediment. Further, the extreme abundance of well-preserved fishes and crustaceans through many metres of rock, some of the bedding planes being completely covered by fishes, is clear evidence of the occasional occurrence of mass mortalities. As a further hypothesis I would propose that these mass mortalities were caused, like the majority of known examples (Brongersma–Sanders, 1957), by toxins released in " waterbloom " conditions, and that the high percentage of silica in the rocks (21% at Hakel, not detrital but colloidal, Roger, 1946 : 77) results from the solution of diatom frustules.

III. THE AGE OF THE CENOMANIAN FISH BEDS

The age of the beds at Hakel and Hajula, though known to be Cenomanian, is not yet precisely fixed stratigraphically but estimated from the fish faunas. d'Erasmo

(1946 : 134) and Arambourg (1954 : 163) both concluded that an Upper Cenomanian age is most probable, and in an earlier paper (Patterson, 1964 : 362) I accepted this estimate. d'Erasmo's conclusion was based on a comparison with the fauna of Comen, near Trieste : he thought that both faunas were Upper Cenomanian in age. Arambourg, describing the fauna of Jebel Tselfat, Morocco, found that it is closest to that of Comen, and that since Comen and Jebel Tselfat share certain archaic genera (*Belonostomus, Thrissops, Clupavus*) which are absent at Hakel and Hajula they are probably Lower Cenomanian in age while the Lebanese localities are Upper Cenomanian. Some new evidence suggests that a re-examination of these conclusions is necessary. The microfauna of Hakel (*Hedbergella* present, no *Globotruncana* or *Rotalipora*) suggests an age low in the Cenomanian according to Dr. D. D. Bayliss (personal commn.), and Dubertret (1963 : 57) speaks of the fish beds at Hakel and Hajula as lying low in the Cenomanian. The more advanced teleosts suggest close relationship between the Lebanese fauna and that of Jebel Tselfat : *Protobrama* (Hajula) is close to *Tselfatia* (Jebel Tselfat) (Patterson, 1967 : 230), *Caproberyx* is present at both Hakel and Jebel Tselfat (p. 98) and *Lissoberyx dayi* (Hakel & Hajula) resembles *Acrogaster anceps* (Jebel Tselfat) (p. 79). Further, one cannot attach much importance to the presence at Comen and Jebel Tselfat of *Belonostomus, Thrissops* and *Clupavus*, which Arambourg holds to be archaic forms absent at Hakel and Hajula. *Belonostomus* occurs rarely at Hakel (P.4029, P.8676) and in any case is of little value as an indicator of age since it ranges upwards to the Maestrichtian. Although *Thrissops* is apparently absent at Hakel and Hajula, *Eubiodectes* (Hay, 1903 : 415) is very similar and possible synonymous (Bardack, 1965 : 35). As I hope to show in a forthcoming paper, *Clupavus* or a related genus is abundant at Hakel and Hajula, although not previously recognized : the species *Clupea gaudryi* Pictet & Humbert (1866 : 60, pl. 5, figs. 2–5) is not a *Scombroclupea* as Smith Woodward (1901 : 138), Kramberger (1895 : 37), d'Erasmo (1922 : 72 ; 1946 : 70) and other authors have supposed since the type material lacks ventral scutes and finlets behind the anal fin. The specimens described as *Scombroclupea gaudryi* by Smith Woodward, d'Erasmo and Kramberger are true *Scombroclupea* but are not conspecific with the type material, which is close to *Clupavus*.

But in spite of this evidence of relationship with the faunas of Comen and Jebel Tselfat, Hakel and Hajula contain some advanced groups which are absent in the Moroccan and Dalmatian localities. The most important of these are the primitive eels (*Urenchelys, Anguillavus* and possibly *Enchelion*) and the Ctenothrissiformes (*Ctenothrissa* and *Pateroperca*). These two groups occur otherwise only in the English Chalk (with the exception of a species of *Anguillavus* in the Kansas Chalk (Martin, 1920 : 95, pl. 6)), whose lower zones are definitely of Upper Cenomanian age. But the Lebanese fauna is almost certainly older than that of the Upper Cenomanian zones of the English Chalk, for it lacks groups such as the specialized ichthyodectids (*Ichthyodectes, Xiphactinus*) which are present there, and contains primitive forms (Clupavidae, *Diplomystus brevissimus*) absent in the Chalk.

In summary, the fauna of Hakel and Hajula is closely related to that of Comen and Jebel Tselfat, Lower Cenomanian in age, but is probably younger than these (eels and ctenothrissoids present). It is also closely related to the fauna of the

Upper Cenomanian zones of the English Chalk, but is probably older than this (clupavids and *Diplomystus brevissimus* present, no advanced ichthyodectids). Pending more precise stratigraphic work in the Lebanon, a Middle Cenomanian age seems most likely for Hakel and Hajula.

IV. SYSTEMATIC DESCRIPTIONS

Order BERYCIFORMES

DIAGNOSIS. See Tate Regan (1911 : 2).

Suborder BERYCOIDEI

DIAGNOSIS. See Patterson (1964 : 433).

Family **TRACHICHTHYIDAE** Bleeker 1895

DIAGNOSIS. See Patterson (1964 : 305).

Genus ***LISSOBERYX*** nov.

DIAGNOSIS. Small Cretaceous Trachichthyidae with the bones of the head without ornament except for weak serrations on the edges of the infraorbitals, preopercular, interopercular and subopercular ; skull roof broad and flat, without ornament, crests or mucus cavities ; supraoccipital crest short and high, supratemporal fossa ending above posterior edge of orbit ; post-temporal fossa partially roofed ; toothless maxilla expanded posteriorly, two supramaxillae, ectopterygoid toothed ; opercular covered by scales ; 23 vertebrae including one ural centrum ; dorsal fin with 5 spines, anal with 4, less than 10 soft rays in each ; scales thin and ctenoid, none enlarged, no ventral ridge scales.

TYPE SPECIES. *Acrogaster dayi* Smith Woodward, 1942.

Lissoberyx dayi (Smith Woodward)

(Pl. 1, fig. 1, Pl. 4, fig. 1 ; Text-figs. 1–3)

1942 *Acrogaster dayi* Smith Woodward : 540, pl. 4, fig. 2.
1964 *Acrogaster dayi* Smith Woodward ; Patterson : 410.

DIAGNOSIS. As for genus, only species : reaching about 4 cm. in standard length ; D V, 9 ; A IV, 8 ; P c. 10 ; V I, 6.

HOLOTYPE. AUB 108930, Day colln., American University, Beirut.

MATERIAL. In addition to the holotype, four specimens, AUB 101997, 107578, 108926 and 109129, Day colln., American University, Beirut.

HORIZON AND LOCALITIES. Middle Cenomanian ; Hajula (4 specimens) and Hakel (1 specimen), Lebanon.

DESCRIPTION. Smith Woodward's original description (1942 : 540) mentions nothing except the proportions of the trunk and the composition of the dorsal and anal fins. The description which follows is based mainly on AUB 107578 (Pl. 4, fig. 1) and 108926 (Pl. I, fig. 1) which have been prepared with acid after embedding in resin. Text-figures 1–3 are composite restorations, based on four specimens.

Measurements and proportions. The dimensions of the five specimens are shown in Table 1.

Table 1.—Dimensions (in mm.) of specimens of *Lissoberyx dayi* (Smith Woodward)

Specimen	Total length	Standard length	Maximum depth	Length of head	Predorsal length	Preanal length
AUB 108930*	48	41	22	16	24	30
,, 101997	32	26	14	12	13	23
,, 107578	—	—	13	10	13	20
,, 108926	40	34	16	15	17	28
,, 109129	44	39	20	15	21	30
mean % standard length	118%	100%	49%	42%	53%	80%

* Corrected measurements from Smith Woodward's figure (1942, pl. 4, fig. 2) of the holotype, which is not natural size as stated but × c. 1·2.

Lissoberyx dayi was a small, deep-bodied fish (Text-fig. 3) reaching about 40 mm. in standard length, 50 mm. in total length. The maximum depth of the trunk is almost exactly half the standard length, the length of the head about 42% of the standard length.

Neurocranium. No details of the basicranium are visible in any specimen but the skull roof (Text-fig. 1) is moderately well exposed in the two acid prepared specimens, although few of the sutures can be seen. The skull roof is short and very broad. It is unlike that of any living berycoid in being quite smooth, without the strong ornament characteristic of the holocentrids or the crests and mucus cavities of the trachichthyids and their relatives. There is a high, triangular supraoccipital crest (*soc.*), thickened anteriorly, which rises from a short, broad supratemporal fossa (*st. f.*). The supratemporal fossa is limited anteriorly and laterally by a low, smooth crest, formed by the frontals anteriorly and the parietals (*pa.*) laterally. The dorsal limb of the extrascapular (*ext.*) articulated with the hind end of the parietal crest and a short groove on the medial face of the crest carried the terminal part of the supratemporal commissural sensory canal, as in many fossil and living berycoids. The limits of the parietals, epiotics and supraoccipital within the supratemporal fossa cannot be distinguished. Lateral to the supratemporal fossa there is a high, narrow post-temporal fossa (*pt. f.*). The post-temporal fossa is partially roofed by the parietal and pterotic (*pto.*), which make contact in the lateral wall of the fossa (108926), as in other Cretaceous berycoids (*Hoplopteryx*, *Trachichthyoides*, *Caproberyx pharsus*: Patterson 1964 : 360, text-figs. 47, 55 : p. 98). This contact between the parietal and pterotic is a relic of the complete roof of the post-temporal fossa in more primitive teleosts. Lateral to the post-temporal fossa the pterotic projects in a broad, smooth wing, continued anteriorly by the sphenotic (*spo.*). On the lower margin of the

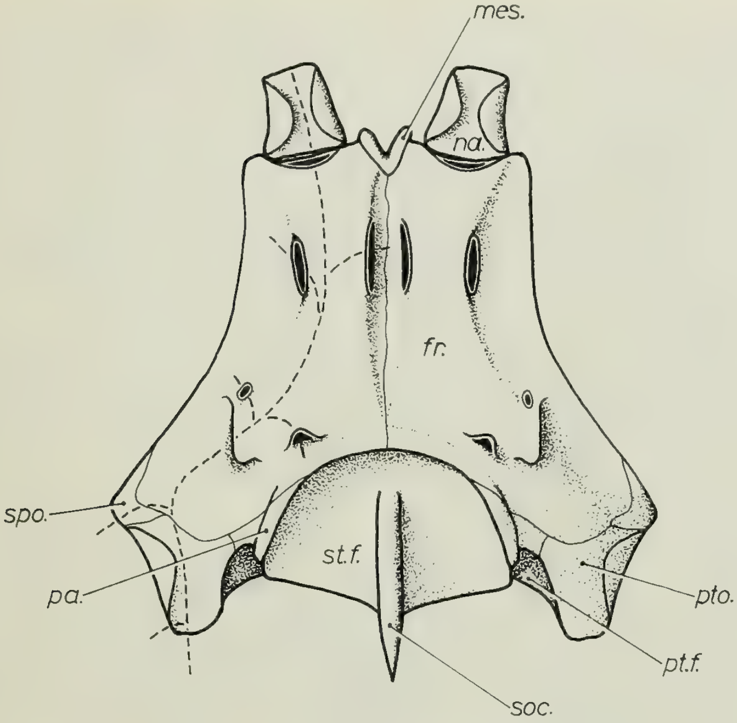

FIG. 1. *Lissoberyx dayi* (Smith Woodward). Restoration of the skull roof in dorsal view, ×8 approx. *fr.*, frontal; *mes.*, mesethmoid; *na.*, nasal; *pa.*, parietal; *pt.f.*, post-temporal fossa; *pto.*, pterotic; *soc.*, supraoccipital; *spo.*, sphenotic; *st.f.*, supratemporal fossa. The broken line on the left side of the figure indicates the course of the sensory canals.

exposed area of the pterotic there is a flange projecting dorsally: this flange carried the main cephalic sensory canal on its dorsal surface, the infraorbital and preopercular canals passing ventrally before and behind it respectively. Below the flange there is a moderately deep dilatator fossa. An exactly similar flange is present in the living holocentrid *Myripristis*.

The major part of the skull roof is formed by the frontals (*fr.*), the two bones together covering an area about as broad as it is long. Each frontal has a broad, smooth supraorbital flange passing back to its junction with the sphenotic. The supraorbital sensory canal, passing on to the frontal from the sphenotic, entered the bone at the level of the front of the supratemporal fossa through an elongated opening covered by a projecting flange of bone. A small pore just in front of this opening transmitted a short branch of the canal on to the supraorbital flange, and a postero-medial branch opened through a larger pore, again covered by a projecting flange, at the foot of the crest bounding the supratemporal fossa. The canal passed to the anterior end of the frontal in a wide tube which opens through two elongated pores above the anterior third of the orbit, one leading laterally on to the supraorbital flange, the other opening into a long, shallow median depression between the frontals. This simple, largely enclosed canal system resembles that in holocentrids like the living *Holocentrus* and *Myripristis* and the Cretaceous *Stichocentrus* and *Caproberyx* (Text-figs. 7, 10); it is quite unlike the system of open mucus cavities found in the trachichthyids and their allies. From a wide opening in the anterior edge of the frontal the supraorbital canal passed forwards to the nasal (*na.*). The nasals are moderately large, smooth bones, tapering forwards, with the lateral and medial edges rolled upwards to form a partially enclosed channel for the sensory canal. The nasals were loosely attached to the frontals, not sutured on as they are in most trachichthyids.

Enclosed between the anterior ends of the frontals is the "V" shaped upper edge of the mesethmoid (*mes.*). The lateral ethmoids (*l.e.*) are deep and very broad. The parasphenoid is deep, broad and without teeth. The vomer is not visible in any specimen, nor can an orbitosphenoid be seen.

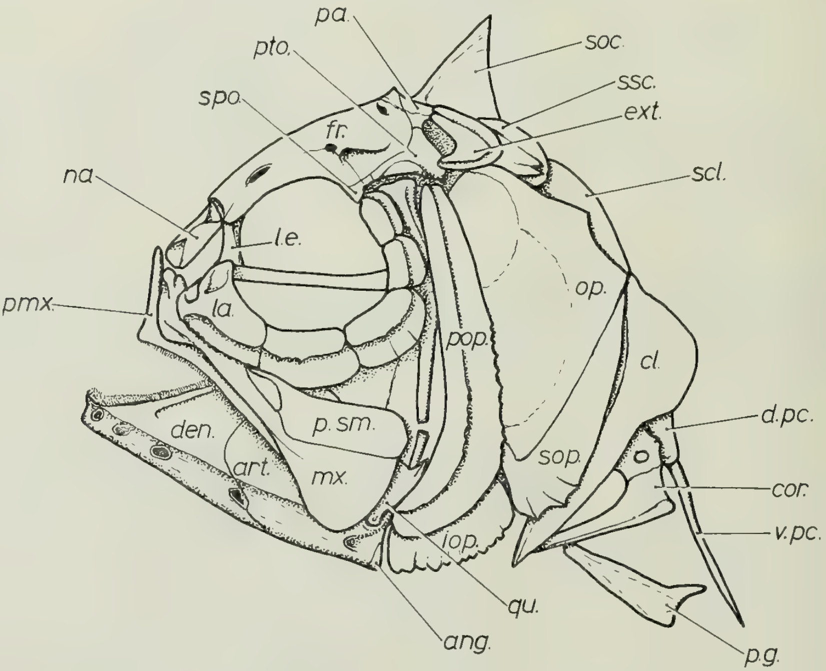

FIG. 2. *Lissoberyx dayi* (Smith Woodward). Restoration of the skull and pectoral and pelvic girdles in left lateral view, ×5 approx. *ang.*, angular; *art.*, articular; *cl.*, cleithrum; *cor.*, coracoid; *den.*, dentary; *d.pc.*, dorsal postcleithrum; *ext.*, extrascapular; *fr.*, frontal; *iop.*, interopercular; *la.*, lachrymal; *l.e.*, lateral ethmoid; *mx.*, maxilla; *na.*, nasal; *op.*, opercular; *pa.*, parietal; *p.g.*, pelvic girdle; *pmx.*, premaxilla; *pop.*, preopercular; *p.sm.*, posterior supramaxilla; *pto.*, pterotic; *qu.*, quadrate; *scl.*, supracleithrum; *soc.*, supraoccipital; *sop.*, subopercular; *spo.*, sphenotic; *ssc.*, suprascapular; *v.pc.*, ventral postcleithrum.

Circumorbital bones. The infraorbital series contains the normal complement of four infraorbitals and a lachrymal. All the infraorbitals are deep (Text-fig. 2), with a deep flange overhanging the groove for the sensory canal. There are a few weak serrations on the edge of this flange on the first and second infraorbitals and two shallow grooves marking branches of the canal on the second infraorbital : the bones are otherwise smooth. There is a broad subocular shelf on the second infraorbital only. The lachrymal (*la.*) is no deeper than the infraorbitals ; dorsally it articulates with the lateral ethmoid by a strong facet. The groove for the sensory canal on the lachrymal is bridged by a bar of bone where it turns upwards anteriorly, and there are a few weak serrations on the ventral edge of the bone. There is no trace of an antorbital but the apparent absence of this small bone could be due to imperfect preservation.

Palate and jaws. The hyomandibular lies almost vertically and is slender, with an undivided head. The symplectic inclines forwards slightly and the condyle of the quadrate (*qu.*) lies below the hind edge of the orbit. The endopterygoid is not toothed. The ectopterygoid is toothed, and although the palatine is not visible in any specimen it will almost certainly have borne teeth, since I know of no acanthopterygian in which a toothed ectopterygoid occurs with a toothless palatine.

The ascending process of the premaxilla (*pmx.*) is about half as long as the toothed alveolar process and is well marked off from the articular process. The maxilla (*mx.*) is about half as long again as the premaxilla and strongly expanded posteriorly, but there are no teeth on the posterior expansion as there are in *Myripristis* and the Cretaceous *Hoplopteryx macracanthus* (Patterson, 1964 : 334) and *Gnathoberyx* (p. 83). There are two supramaxillae, the posterior (*p. sm.*) with a slender process overlying the anterior. The mandible is long and deep, both the dentary (*den.*) and the articular (*art.*) forming a high coronoid process, that of the dentary toothed throughout its length. At the symphysis the band of teeth on the dentary becomes broader but does not extend on to the lateral face of the bone as it does in some berycoids. At the back of the mandible there is a very small angular (*ang.*). The mandibular sensory canal ran in a closed tube opening by three pores in the dentary and a pore at the suture between dentary and articular. All the bones of the jaws are without ornament.

Opercular bones. The preopercular (*pop.*) is long, broad, inclined backwards a little and weakly angulate. There are weak serrations on the posterior edge of the lower half of the vertical limb and a few serrations above the angle in the bone on the edge of the flange overhanging the groove for the sensory canal. The opercular (*op.*) is smooth, but has two weak spines on its posterior edge. The opercular is covered by scales : two very large cycloid scales cover the anterior part of the bone with three or four smaller scales on the posterior part (101997, 107578). The subopercular (*sop.*) has the normal spike overlapping the ventral corner of the opercular, and three ridges, each ending in a serration, on its ventral edge. The interopercular (*iop.*) bears a number of weak ridges ending in feeble serrations along its ventral edge.

Hyoid arch and branchiostegals. The ceratohyal is ossified in the usual two pieces ; the distal ossification is very deep and is perforated by a large oval fenestra. There are seven branchiostegals, three articulating with the medial face and two with the lateral face of the distal ceratohyal, and two articulating the lateral face of the proximal ceratohyal.

Vertebral column. There are 23 vertebrae, 9 abdominal and 14 caudal, including one free ural centrum (the second). Ribs are present on all the abdominal vertebrae except the first, and are borne on transverse processes on the last four (five in 101997). There are no epineurals or epipleurals. The caudal skeleton will not be described in detail here since I am dealing with the caudal skeletons of all Cretaceous Beryciformes in a forthcoming paper : suffice it to say that the caudal of *Lissoberyx* agrees with that of the living trachichthyid *Hoplostethus* (Gosline, 1961 : 14) in having a neural crest on the second pre-ural centrum and a free second ural centrum.

Pectoral and pelvic girdles and fins. The pectoral girdle contains the normal complement of bones, a curved extrascapular (*ext.*) articulating with the parietal above and the pterotic below, a forked suprascapular (*ssc.*) articulating with the epiotic and intercalar, a blade-shaped supracleithrum (*scl.*), a large, sigmoid cleithrum (*cl.*), two post-cleithra, the upper (*d. pc.*) scale-like, the lower (*v. pc.*) rod-like, and the scapula and coracoid. All the dermal bones of the girdle are smooth and unornamented. The anterior process of the coracoid (*cor.*) is moderately stout and long, arching forwards to join the cleithrum just above its tip. The pectoral fin contains about ten rays.

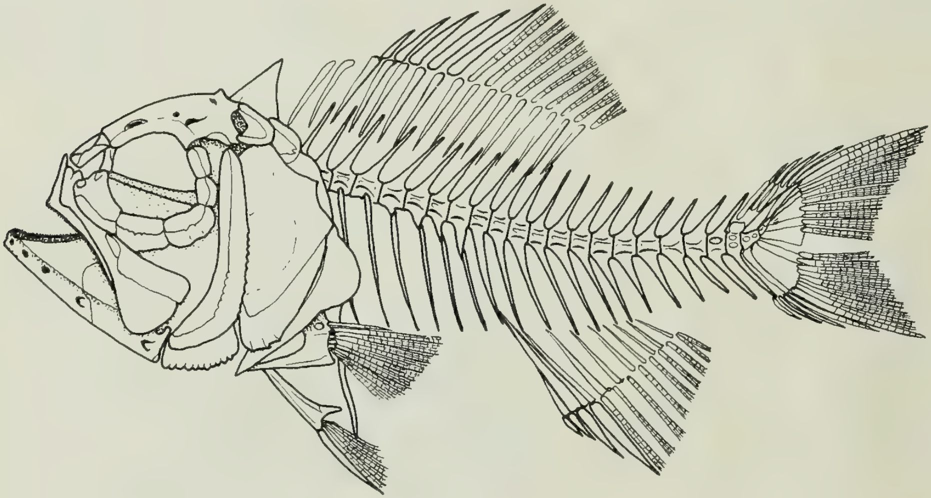

FIG. 3. *Lissoberyx dayi* (Smith Woodward). Restoration of the skeleton, scales omitted, ×2·5 approx.

The pelvic fins are thoracic, the fin originating well in front of the tip of the ventral post-cleithrum and the girdle (*p. g.*) ending between the anterior processes of the coracoids. The pelvic fin contains a stout, smooth spine and six soft rays.

Median fins. The dorsal fin originates above the pelvic and occupies little more than half the back of the fish ; it contains five smooth spines, increasing in length from front to rear, and 9 soft rays. The longest spine is equal in length to the distance between the base of the fin and the vertebral column. The first radial of the fin is not enlarged, and lies between the neural spines of the second and third vertebrae. There are two predorsals (Smith & Bailey, 1961) in front of the fin. The anal fin arises below the hind end of the dorsal ; it contains four spines, increasing in length, and 8 soft rays. The fourth anal spine is equal in length to the fifth dorsal spine. The first anal radial is very small and the second is only a little enlarged.

The forked caudal fin contains 19 principal rays with 17 branched, 9 in the upper lobe and 8 in the lower. Preceding the upper lobe there are four small spines and one segmented ray, preceding the lower three spines and a segmented ray.

Squamation. The scales are large, thin and coarsely ctenoid. There are 13 scales in a transverse series on the trunk, the lateral line passing through the fifth from the top. The lateral line scales are not enlarged. Scales cover the cheek and the opercular, but the scales do not extend over the bases of the fins. There are no ventral ridge scales.

AFFINITIES. Smith Woodward (1942 : 540), in his original brief description of *Lissoberyx dayi*, placed the species in the trachichthyid genus *Acrogaster*. Clearly the species cannot be included in this genus : in *Acrogaster* the skull roof bears a normal trachichthyid system of large mucus cavities separated by high, serrated crests, the alveolar process of the premaxilla is almost as long as the maxilla and the maxilla is not expanded behind it, the preopercular bears a number of large spines at the angle, there are no scales on the operculum, there are eight branchiostegals and the scales are cycloid (Patterson, 1964 : 410). In all these characters *A. dayi* differs from the Senonian species of the genus, and since it shows no signs of close relationship with any other Cretaceous genus it is necessary to make a new genus to receive it. The name *Lissoberyx* refers to the smooth skull roof and general absence of ornament on the head. *Acrogaster anceps* Arambourg (1954 : 153), known by a single specimen from the Lower Cenomanian of Morocco, is probably another species of *Lissoberyx* : it agrees with *L. dayi* and differs from the Senonian species of *Acrogaster* in having the maxilla expanded posteriorly, in the small number of vertebrae (21) and in the form of the dorsal and anal fins. Through the kindness of Prof. J. P. Lehman and Mlle. J. Signeux I was able to examine this specimen and could find no trenchant differences from *L. dayi*. Although Arambourg found traces of two or three spines on the angle of the preopercular he spoke of these as " assez fruste " : to me it appears that these traces are not spines but ridges on the surface of the bone marking branches of the sensory canal. Arambourg described the pelvic as containing 7 or 8 soft rays, a difference from *L. dayi* and all trachichthyids, but in my opinion the pelvic fins are not sufficiently well preserved for an accurate count to be made.

That *Lissoberyx dayi* is a member of the Beryciformes is shown by the presence of fin spines, pelvics with more than five soft rays, two supramaxillae and a nineteen-rayed tail. Within the Beryciformes *Lissoberyx* falls in the sub-order Berycoidei (Patterson 1964 : 433) because of the toothless endopterygoid, the absence of epineurals, the pelvic spine and the nineteen-rayed caudal. All known Cretaceous Berycoidei are members either of the Trachichthyidae or the Holocentridae, and there is normally no difficulty in deciding to which of these two families a genus belongs. However, as the Trachichthyidae and Holocentridae are traced back to the Cenomanian they begin to converge, holocentrid characters such as maxillary teeth and an antorbital appearing in the trachichthyid *Hoplopteryx* and trachichthyid characters such as a small number of dorsal fin spines, a large supraoccipital crest and a supratemporal fossa appearing in the holocentrid *Caproberyx* (Patterson, 1964 : 341, 359 ; p. 102). In *Lissoberyx* this trend goes further : the fish is a mosaic of trachichthyid and holocentrid features.

First, there are several characters of *Lissoberyx* which are common to both trachichthyids and holocentrids in the Cretaceous, though not always to living members of these families. These include the partial roof over the post-temporal fossa (as in *Hoplopteryx*, *Trachichthyoides* and *Caproberyx pharsus*, p. 98), the presence of ectopterygoid teeth, two supramaxillae (only one in living trachichthyids), the mandibular sensory canal running in a canal opening by three or four pores (as in Cretaceous but not living holocentrids), the preopercular without a spine at the angle, the deep, perforate ceratohyal (as in Cretaceous but not in living holocentrids), the presence of predorsals in front of the dorsal fin and the insertion of the first dorsal radial between the second and third neural spines (as in *Hoplostethus* and living holocentrids), the four anal fin spines and the unmodified anal radials (the third anal spine is enlarged in most holocentrids, but not in *Caproberyx*) and the unspecialized ctenoid scales.

Secondly, there is a group of characters in which *Lissoberyx* resembles the trachichthyids and differs from the holocentrids. These include the high supraoccipital crest and moderately large supratemporal fossa (a similar supraoccipital crest occurs in the holocentrids *Caproberyx* and *Stichocentrus*, Text-figs. 8, 10, but there the supratemporal fossa is much smaller), the deep infraorbitals with the lachrymal no deeper, the subocular shelf on the whole of the second infraorbital (as in *Hoplopteryx* but not in living trachichthyids), the 23 vertebrae (the vertebral number never seems to fall below 26 in holocentrids), the six soft rays in the pelvic fin (7 in holocentrids except in *Caproberyx pharsus*, p. 102), and the form of the dorsal fin, with five spines and nine soft rays (no holocentrid is known to have less than six spines and eleven soft rays).

Thirdly, characters in which *Lissoberyx* resembles the holocentrids and differs from the trachichthyids include the absence of large mucus cavities on the skull roof and the pattern of the supraorbital sensory canal (as in *Myripristis*), the form of the pterotic (again as in *Myripristis*), the nasals not sutured to the frontals or to each other, the unreduced mesethmoid, the short alveolar process of the premaxilla and the strongly expanded maxilla, the presence of scales on the operculum (though in Cretaceous holocentrids only the antero-dorsal corner of the opercular is scaly), and the rather long and stout anterior process of the coracoid.

Finally, there are a few characters in which *Lissoberyx* differs from both the trachichthyids and the holocentrids. These are the smoothness of the skull roof and the almost complete absence of ornament on the bones of the head, the seven branchiostegal rays (eight in both trachichthyids and holocentrids) and the complete scaly covering of the opercular.

Evaluation of this complex of characters is difficult : the characters in each group cannot simply be counted because they obviously differ in significance. On balance, I feel sure that *Lissoberyx* lies nearer to the trachichthyids than to the holocentrids, particularly significant associations with the trachichthyids being the supratemporal fossa, the form of the infraorbitals, the number of vertebrae and the dorsal and pelvic fins. But the most important features in which *Lissoberyx* resembles the holocentrids, the characters of the skull roof and the upper jaw, are almost certainly primitive, since the deep mucus cavities of the trachichthyid skull roof can hardly be anything but specialized and since a short premaxilla and an expanded maxilla are more likely to be primitive than a premaxilla extending to the tip of the maxilla (Patterson, 1964 : 439). Of the characters in which *Lissoberyx* differs from both holocentrids and trachichthyids, the smooth skull roof and absence of ornament on the head must be primitive while the seven branchiostegals are advanced. The scaly opercular is probably primitive for the berycoids (see below p. 107). It may be significant that in the seven branchiostegals and the scaly opercular (as also in the lack of ornament and the unreduced mesethmoid) *Lissoberyx* resembles the Berycidae (particularly *Beryx*), a group probably derived from the trachichthyids.

The presence of ribs on all but the first abdominal centrum in *Lissoberyx* is a peculiar feature which is otherwise known only in *Stichocentrus* (p. 93) among Beryciformes. In acanthopterygians the first two vertebrae normally bear only slender bones which appear to be in series with the epipleurals rather than the ribs (Starks, 1904 : 616 ; Gosline, 1963 : 28). It may be that in *Lissoberyx* an anterior centrum has become incorporated in the neurocranium, but the fact that the first dorsal radial lies between the second and third neural spines in *Lissoberyx*, *Hoplostethus*, *Stichocentrus* and living holocentrids suggests that the first free vertebra is homologous in all these forms. It is also possible that the slender bones borne on the first two vertebrae of some acanthopterygians are not epipleurals but reduced ribs : the skeletons of living Beryciformes that I have examined suggest that this may be true of trachichthyids and some holocentrids. In any event, Rosen (1964 : 242) shows that differences in the point of origin of the first rib cannot be interpreted in the simplest terms in teleosts.

In summary, *Lissoberyx* is a trachichthyid, but it shows more resemblance to the holocentrids than any other trachichthyid and must lie very close to the common stock of these two families and of the sub-order Berycoidei. As the most generalized member of this sub-order, *Lissoberyx* throws some light on the origin of the group and is discussed further on p. 106 below.

Genus ***GNATHOBERYX*** nov.

Diagnosis. Small Cretaceous Trachichthyidae in which the maxilla is toothed and forms more than half the gape ; superficial bones of the head and scales spiny ; long, slender teeth in the upper jaw, supramaxillae reduced or absent ; 27 vertebrae, including a free second ural centrum ; dorsal and anal fin each with four spines and less than ten soft rays ; scales ctenoid and spiny, lateral line scales enlarged and thickened, ventral ridge scales present.

Type species. *Gnathoberyx stigmosus* sp. nov.

Gnathoberyx stigmosus sp. nov.

(Pl. 1, fig. 2, Pl. 2 ; Text-figs. 4, 5)

Diagnosis. As for genus, only species : reaching about 4 cm. in standard length, depth of trunk about 45% of standard length, length of head about 35% of standard length ; D IV, 9 ; A IV, 8.

Holotype. AUB No. 100402 (Pl. 1, fig. 2, Pl. 2, fig. 2).

Material. In addition to the holotype, AUB No. 103838 (Pl. 2, fig. 1).

Horizon and locality. Upper Senonian ; Sahel Alma, Lebanon.

Description. Acid preparation has not been used on this species because there are only two specimens and material from Sahel Alma often gives poor results in transfer preparations. For this reason much of the cranial anatomy remains unknown at present.

Measurements and proportions. The dimensions of the two specimens are as follows (in mm.), the first figure in each case being for the holotype, the second for 103838 : total length : 50–52, standard length : 40–c. 42, maximum depth of trunk : c. 20–18, length of head : 16–15, predorsal length : 21–23, preanal length : c. 28–27.

Although both specimens are distorted, 103838 by oblique crushing, the holotype by displacement of the anal fin and deepening of the trunk, they are clearly closely comparable in size. *G. stigmosus* was a small, deep-bodied fish, about 40 mm. in standard length, with the maximum depth of the trunk about 46% of the standard length and the length of the head about 35% of the standard length.

Neurocranium. The skull roof is not well exposed in either specimen. The supraoccipital crest was low, not projecting above the skull roof, and apparently

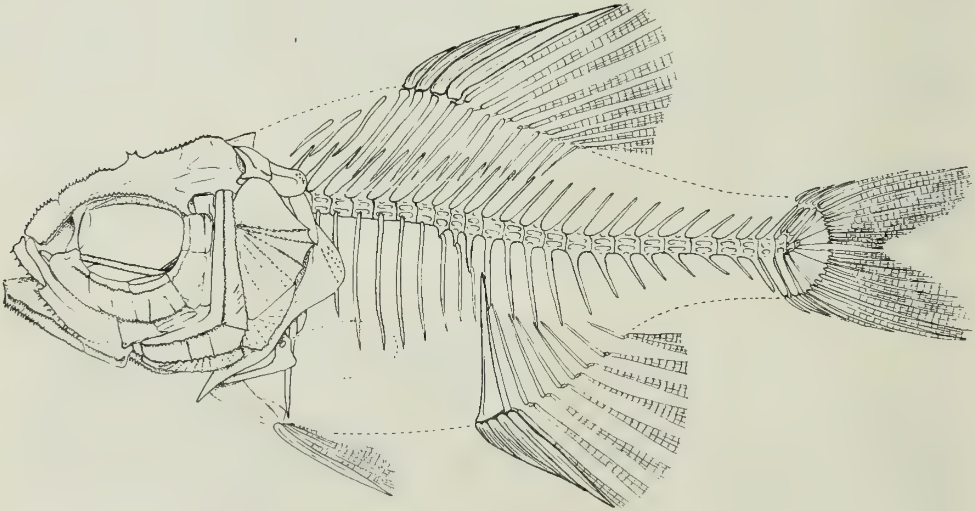

Fig. 4. *Gnathoberyx stigmosus* gen. et sp. nov. Restoration of the skeleton, scales omitted, × 2·5 approx.

rather short, arising at the level of the hyomandibular facet. The skull roof bore a pattern of high crests bounding mucus cavities, as is normal in trachichthyids, but the details of the pattern cannot be made out. The lateral margin of the frontal above the orbit bears a row of large, pointed spines and there is a more medial crest bearing similar spines which is continued back by the parietal. The postero-lateral part of the skull roof is smooth and without ornament. The nasals are large, thick, scroll-like bones, probably sutured to the frontals, with coarse spines on their margins. The nasals extend antero-ventrally almost to the vomer, indicating that in this species, as in *Hoplopteryx* and living trachichthyids, the mesethmoid was much reduced. These facts suggest that the skull roof of *Gnathoberyx* was of the same type as in *Hoplopteryx* and *Hoplostethus* (Patterson, 1964, text-figs. 46, 54, 65), and that the supratemporal fossa was short, as in Trachichthyidae, not extended forwards as it is in Berycidae.

An orbitosphenoid is not visible in either specimen. The parasphenoid is straight and slender, and there is a long basisphenoid pedicel articulating with it at the hind edge of the orbit. No details of the otic region are visible.

Infraorbital bones. The infraorbitals are very deep, as deep as or deeper than the lachrymal. Dorsally they bear a thickened, serrated flange projecting over the groove for the sensory canal and the ventral edges are also coarsely serrated. The subocular shelf is confined to the second infraorbital. All these features are typical of trachichthyids. There is no trace of an antorbital.

Palate and jaws. The hyomandibular is inclined posteriorly a little but the quadrate and the elongated symplectic are inclined forwards so that the articular condyle of the quadrate lies only just behind the centre of the orbit, and the gape is shorter than in most trachichthyids. The endopterygoid is toothless, as usual in Berycoidei. There is a long patch of teeth on the border of the anterior part of the palate, but whether these teeth extend on to the ectopterygoid or are all on the palatine cannot be seen. There is a normal maxillary process on the tip of the palatine.

The upper jaw (Text-fig. 5, Pl. 2, fig. 2) is remarkable in having a long, toothed maxilla which makes up more than half of the gape. The premaxilla is not well preserved in either specimen and the details of the head of the bone cannot be made out, but the ascending process was clearly very small, no higher than and probably hardly distinct from the articular process. The alveolar process, extending back below the maxilla, bears minute clustered teeth on its ventro-medial surface and a single irregular row of six or seven long, slender teeth along its outer margin. On the dorsal surface of the alveolar process there is a low, rounded postmaxillary process lying medial to the maxilla. The total length of the premaxilla is about 40% of the length of the maxilla. As in the premaxilla, the articular head of the maxilla is not well preserved. Above the alveolar process of the premaxilla the maxilla extends back as a stout rod which deepens abruptly at the hind end of this process ; along the margin of this deep posterior part of the maxilla there is a single irregular series of about a dozen long, slender teeth, the anterior ones curved forwards. The anterior end of the toothed border of the maxilla projects forwards medial to the tip of the premaxilla in exactly the same way as in the ctenothrissiform *Aulolepis*

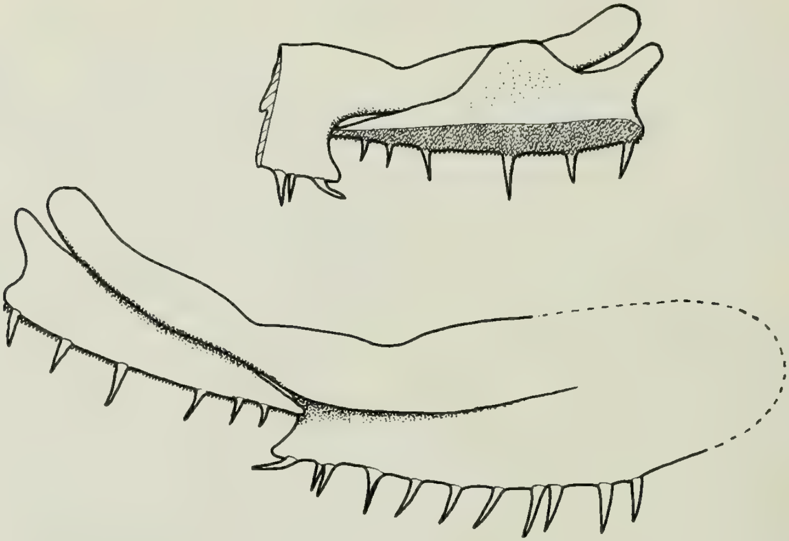

FIG. 5. *Gnathoberyx stigmosus* gen. et sp. nov. Left upper jaw. Below, in lateral view; above, the anterior part of the jaw in medial view. × 12 approx.

(Text-fig. 6B). On the outer face of the toothed part of the maxilla there is a groove, overhung by a flange anteriorly, which closely resembles the groove in *Ctenothrissa* which I (Patterson, 1964 : 232; Text-fig. 6A) interpreted as housing a ligament attaching the upper jaw to the mandible. The hind end of the maxilla is not completely preserved in either specimen: the bone evidently became much thinner and was without teeth. The dorsal edge of the toothed part of the maxilla is thin and smooth so far as it is preserved, and in neither specimen is there any trace of supramaxillae: if these were present they must have been small and flimsy, not like the large supramaxillae of Ctenothrissiformes and most Berycoidei. In contrast to most of the superficial bones of the head, the upper jaw is smooth and without ornament.

The head of the quadrate lies almost below the centre of the orbit, and the mandible is rather short. The ventral edge of the dentary and the flange overhanging the groove for the sensory canal on both the dentary and articular are produced into large, closely packed, recurved spines. In size and shape these spines resemble the large marginal teeth of the upper jaw, but differ from them in having no pulp cavity. The oral border of the dentary bears small, clustered teeth, apparently with a single large procumbent tooth at the symphysis. Whether the mandibular sensory canal ran in a closed tube or in an open groove cannot be seen.

Opercular bones. The preopercular is typically trachichthyid, but because of the forward position of the suspensorium the ventral limb is about half as long as the dorsal and the angle in the bone is acute, almost 90°. The bone is broad throughout its length and, as usual in Cretaceous trachichthyids, without a spine at the angle.

At and below the angle in the bone there are three stout ridges ending in marginal spines, with similar spines spaced out between them, and above the angle there are several shorter radiating ridges.

The opercular is without scales (except perhaps at its antero-dorsal corner, which is not visible) and has a series of stout, spiny ridges radiating from its point of suspension and ending in spines on the edge of the bone. The subopercular bears similar spiny ridges radiating from its antero-dorsal corner, and on the elongated interopercular there are rows of spines radiating from the centre of the bone.

Hyoid arch and branchiostegals. No details of the hyoid skeleton are visible in either specimen. There are eight branchiostegal rays, the first three with coarse spines along their ventral edges.

Vertebral column. There are eleven abdominal vertebrae and sixteen caudals, including a free second ural centrum. The ribs are small and intermuscular-like on the first three abdominal vertebrae and are borne on transverse processes on the last three. There are no epineurals and no epipleurals are visible. The caudal skeleton is preserved only in the holotype ; although it is compressed and distorted it appears to agree with that of the living trachichthyid *Hoplostethus* (Gosline, 1961 : 14) in having no neural spine on the second pre-ural centrum, a slender urodermal " wedged into " the first pre-ural centrum and a separate second ural centrum, which appears larger than that of *Hoplostethus*.

Pectoral and pelvic girdles and fins. There is a broad extrascapular of the usual triradiate form and a forked suprascapular with a long dorsal limb and a few spines near its postero-dorsal corner. The supracleithrum is not clearly visible in either specimen. The posterior plate of the cleithrum bears a few spiny ridges and small spines near its posterior edge. Both the endoskeletal pectoral girdle and the pectoral fin are poorly preserved in the holotype, and in 103838 they are missing. The anterior process of the coracoid appears to have been short and slender, meeting the cleithrum well above its tip. The ventral postcleithrum reaches the ventral border of the trunk just behind the origin of the pelvic fin and the pelvic girdle probably made contact with the cleithrum. The pelvic girdle and fin are missing in 103838 and in the holotype only the spine of the pelvic fin is visible ; it is ridged and equal in length to about one-third of the depth of the trunk.

Median fins. The dorsal fin contains four stout spines, strongly ridged and increasing in length from front to rear, and nine soft rays. The fourth dorsal spine is equal in length to about 55% of the maximum depth of the trunk. The first dorsal radial lies between the third and fourth neural spines and is preceded by three predorsals, one in front of each of the first three neural spines. Except for the first two and last three dorsal radials (two to each vertebra) there is a one-to-one relationship between the fin supports and the vertebrae.

The anal fin contains four stout, ridged spines and eight soft rays. The fourth anal spine is equal in length to about half the depth of the trunk. The first anal radial is enlarged but not hooked forwards distally. The last anal radial lies in front of the fifth haemal spine.

The caudal fin is almost entirely missing in 103838. In the holotype only the upper lobe of the fin is preserved. This contains three small spines, one short segmented ray and ten principal rays, the outermost unbranched. The presence of nine branched rays in the upper lobe is normal in caudal fins with seventeen branched rays.

Squamation. The body scales are thin but coarsely ctenoid and spiny, with their exposed surfaces covered with small spines. The lateral line scales are enlarged and thickened, each with a raised, ornamented bridge covering the sensory canal. There is a series of enlarged, thickened and coarsely ornamented ridge scales along the ventral border of the trunk in front of the anal fin, with a pair of enlarged, thickened and ornamented axillary scales at the origin of the pelvic fins. The dorsal ridge scales in front of the dorsal fin also appear to be slightly thickened. The scales do not cover the median fins but form a sheath along their bases, as in *Trachichthys*. The scales cannot be counted exactly, but they were clearly larger below the enlarged lateral line scales. There were about thirteen scales in each transverse series, with about six below and above the lateral line. Scales cover the cheek.

AFFINITIES. *Gnathoberyx* is shown to be a member of the sub-order Berycoidei by the presence of fin spines, a pelvic spine, eight branchiostegal rays, a caudal skeleton with a free second ural centrum and a caudal fin with seventeen branched rays. Within the Berycoidei the genus falls in the Trachichthyidae because of the form of the skull roof, the deep infraorbitals with a subocular shelf only on the second, the broad, cavernous preopercular, the short dorsal and anal fins, and the enlarged lateral line scales and ventral ridge scales.

The species shows various resemblances to other trachichthyids, living and fossil, such as the spiny head bones and scales (cf. *Hoplopteryx spinulosus*, also from Sahel Alma), the enlarged lateral line scales (cf. *Tubantia* from the Campanian of Westphalia and the living genera *Gephyroberyx* and *Hoplostethus*), and the short dorsal and anal fins, with four spines and less than ten soft rays (cf. *Tubantia* and *Lissoberyx* among Cretaceous forms). But the structure of the upper jaw, with a long, toothed maxilla apparently without supramaxillae, clearly sets the species apart from all other berycoids and makes a new genus necessary to receive it. The upper jaw of *Gnathoberyx*, improbable as it is in a genuine acanthopterygian, is not entirely out of place in the Berycoidei, for maxillary teeth are already known in the living *Myripristis* and the Cretaceous *Hoplopteryx macracanthus* (Patterson, 1964 : 439 ; Text-fig. 6E, F). In these forms, however, the maxilla hardly enters the gape, forming less than a quarter of the margin of the jaw. In *Gnathoberyx* the maxilla is the dominant bone in the upper jaw, in typical clupeiform or protacanthopterygian (Greenwood, Rosen, Weitzman & Myers, 1966) fashion. In particular there are striking resemblances to the upper jaw of the Ctenothrissiformes *Aulolepis* and *Ctenothrissa* (Text-fig. 6A, B), and also to the upper jaw in the living *Macristium* (Text-fig. 6C) which Marshall (1961) has suggested is a living ctenothrissoid, a hypothesis which I earlier (Patterson, 1964 : 243) felt to be unproven. The similarities between the upper jaws of *Gnathoberyx* and *Macristium* extend to the form of the premaxillary teeth and the apparent absence of supramaxillae. Without more material of *Gnathoberyx* it is impossible to study the articular heads of the premaxilla and maxilla to discover whether these resemblances are more than superficial, but in view

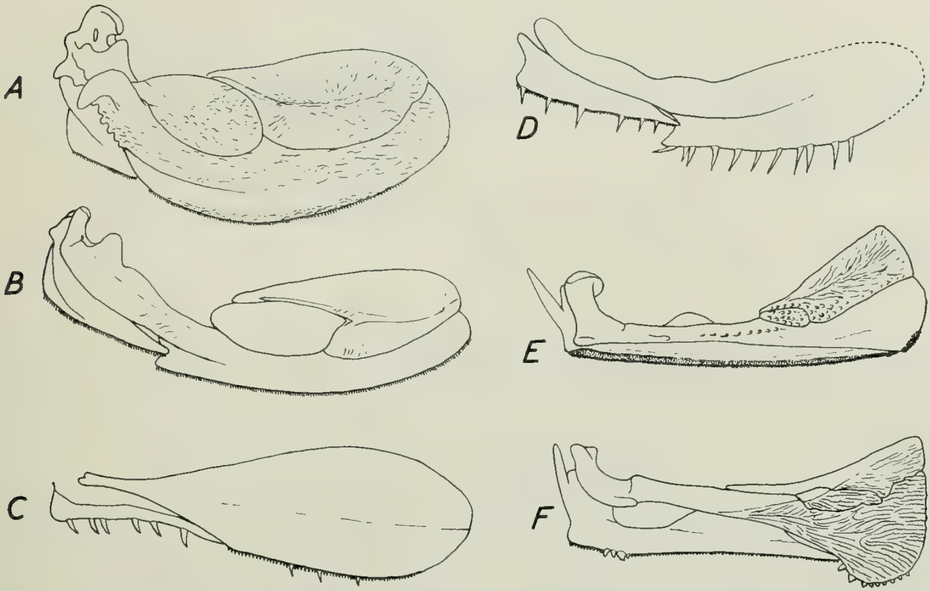

FIG. 6. The left upper jaw in lateral view of Ctenothrissiformes (left) and Berycoidei (right). *A. Ctenothrissa radians* (Agassiz), Ctenothrissidae, Upper Cenomanian, S.E. England, ×1·5. *B. Aulolepis typus* Agassiz, Aulolepidae, Upper Cenomanian, S.E. England, ×2. *C. Macristium chavesi* Tate Regan, Macristiidae (? Ctenothrissiformes), Extant, Atlantic, ×27. After Marshall, 1961. *D. Gnathoberyx stigmosus* gen. et sp. nov., Trachichthyidae, Upper Senonian, Sahel Alma, Lebanon, ×8. *E. Hoplopteryx macracanthus* Patterson, Trachichthyidae, Senonian, S.E. England, ×1·5. *F. Myripristis murdjan* Forskael, Holocentridae, Extant, Red Sea, ×1·6.

of the evidence that the Ctenothrissiformes lie closer than any other group to the ancestry of the Beryciformes (Patterson, 1964 : 463–466 ; Greenwood *et al.*, 1966 : 369) they must be carefully considered. There can be little doubt that the maxillary dentition of *Gnathoberyx* is primitive, not secondary. In *Hoplopteryx macracanthus* and *Myripristis* there is every reason to believe that this is true (Patterson, 1964 : 440), and the argument receives added force from the well-toothed maxilla of *Gnathoberyx*. But it is possible that the upper jaw of *Gnathoberyx* is specialized, for whatever purpose, by reduction in the ascending process of the premaxilla and elongation of the toothed part of the maxilla, secondarily producing a ctenothrissiform type of jaw from a more typical berycoid one. Some support for this hypothesis may be found in the relatively late age of *Gnathoberyx* (U. Senonian compared with the first trachichthyids in the L. Cenomanian) and in the generally specialized aspect of the fish—abundant spiny ornament, enlarged lateral line and ventral ridge scales, the short gape, reduced or lost supramaxillae and large marginal teeth in the upper jaw. And in one respect, the presence of a well developed postmaxillary process on the premaxilla, the upper jaw of *Gnathoberyx* is clearly advanced over those of the Ctenothrissiformes and resembles normal acanthopterygians. These facts suggest that the resemblance between the upper jaws of *Gnathoberyx* and the Ctenothrissiformes is not necessarily evidence of close relationship, but this resemblance certainly adds to the evidence supporting the hypothesis that the Beryciformes evolved from near the Ctenothrissiformes rather than from the myctophoids, in which the maxilla is never toothed.

Family **HOLOCENTRIDAE** Richardson 1846

Diagnosis. See Patterson (1964 : 341).

Subfamily **CAPROBERYCINAE** nov.

Diagnosis. See p. 97.

Genus ***STICHOCENTRUS*** nov.

Diagnosis. Cretaceous Holocentridae with a moderately high supraoccipital crest projecting above the skull roof, frontals covering the anterior part of the parietals, small mucus cavities on the skull roof ; nasals small and tubular ; no antorbital, infraorbitals moderately deep, lachrymal large and deep, not extending back below the first infraorbital, no subocular shelf on first infraorbital ; superficial bones of the head (except the maxilla) ornamented with ridges, spines and tubercles ; head of hyomandibular broad and single, suspensorium inclined backwards a little, ectopterygoid toothed, no maxillary teeth ; no spine on the preopercular ; 26 vertebrae, no free ural centrum ; nine dorsal spines, the last four decreasing in length a little but dorsal fin not divided, five anal spines, the fourth thicker than the fifth but a little shorter ; scales large, rough and ctenoid, abdominal ridge scales present.

Type species. *Stichocentrus liratus* sp. nov.

Stichocentrus liratus sp. nov.

(Pl. 3 ; Text-figs. 7–9)

Diagnosis. As for genus, only species. Reaching about 7 cm. in standard length ; D IX, 11 ; A V, 9 ; P. 11 ; V I, 7.

Holotype. B.M. (N.H.) No. P.47835 (Pl. 3).

Material. In addition to the holotype, seven specimens in the Day Colln., American University, Beirut, AUB 105736, 105987, 106809, 108923–24, 108927, 108929.

Horizon and locality. Middle Cenomanian ; Hajula, Lebanon.

Description. The description and figures are based mainly on the holotype and AUB 108924 which have been prepared with acid after embedding in resin.

Measurements and proportions. The dimensions of the more complete specimens are given in Table 2.

TABLE 2.—Dimensions (in mm.) of the five most complete specimens of *Stichocentrus liratus* gen. et sp. nov.

Specimen	Total length	Standard length	Maximum depth	Length of head	Predorsal length	Preanal length
P.47835	76	64	32	30	29	54
AUB 105736	56	44	—	22	20	37
,, 105987	50	42	19	19	19	—
,, 106809	—	c.74	—	c.35	—	c.57
,, 108929	c.41	c.34	c.17	c.15	—	c.25
mean % standard length	121%	100%	48%	46·5%	45%	78%

Stichocentrus liratus was a small, moderately deep-bodied fish of normal berycoid form (Text-fig. 9). The largest specimen, AUB 106809, is very incomplete but must have had a standard length of about 74 mm. : this would give a total length of about 90 mm. The length of the head and the maximum depth of the trunk are approximately equal, about 47% of the standard length.

Neurocranium. The neurocranium is typically holocentrid in shape, broad and deep posteriorly and tapering forwards. The skull roof (Text-fig. 7) is well exposed in the holotype and 108924. There was a moderately large supraoccipital crest (*soc.*) with a thickened anterior edge ; the crest is higher and longer than it is in living holocentrids, but not so large as it is in *Caproberyx* (Patterson, 1964, text-fig. 67 ; Text-fig. 10). The supraoccipital crest arises from a short, broad, shallow supratemporal fossa (*st. f.*), limited anteriorly by the frontals and parietals. Again, the fossa is larger than it is in living holocentrids but smaller than in *Caproberyx*. The parietals (*pa.*) are separated by the supraoccipital and bear a raised area, ornamented with ridges and tubercles ; the parietal branch of the supraorbital sensory canal opened through a pore in the frontal immediately in front of this area, and passed into a depression on the parietal from which two short grooves, the medial one bifurcated, lead on to the ornamented area. The parietals bear very similar grooves and depressions in the living holocentrid *Holotrachys*. The supratemporal articulated with the hind edge of this ornamented area, transmitting the terminal part of the supratemporal commissural sensory canal, which ran in a short groove behind the ornamented area. It is possible that the parietal met the pterotic in the wall of the post-temporal fossa (*pt. f.*), but the area where the two bones would have made contact is covered by a posterior extension of the frontal. The ventral limb of the supratemporal articulated with the pterotic (*pto.*), and the main cephalic sensory canal passed forwards in a groove covered laterally by a smooth raised flange on this bone. The preopercular sensory canal passed ventrally through a notch at the hind end of this flange. The sphenotic (*spo.*) has the dermal and cartilage components completely fused. The infraorbital sensory canal passed ventrally between two raised, ornamented flanges on the sphenotic.

The frontals (*fr.*) are very large, extending posteriorly to cover much of the parietals and pterotics, a characteristic holocentrid feature. In *Stichocentrus* this posterior extension of the frontals is not so marked as it is in living holocentrids but

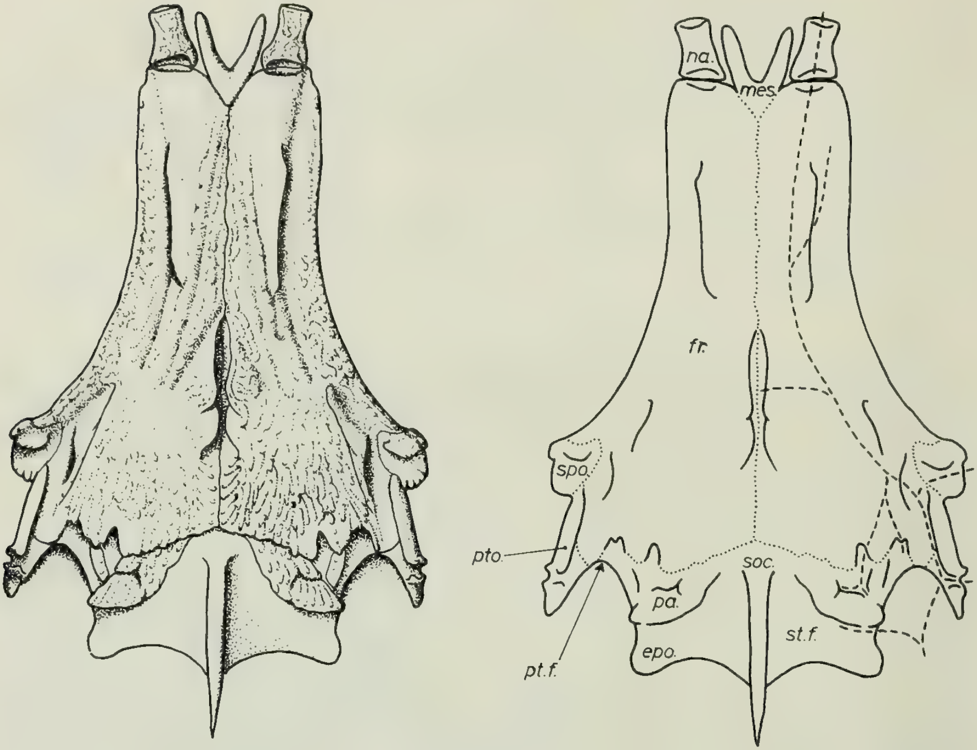

Fig. 7. *Stichocentrus liratus* gen. et sp. nov. Restoration of the skull roof in dorsal view, ×5 approx. *epo.*, epiotic; *fr.*, frontal; *mes.*, mesethmoid; *na.*, nasal; *pa.*, parietal; *pt.f.*, post-temporal fossa; *pto.*, pterotic; *soc.*, supraoccipital; *spo.*, sphenotic; *st.f.*, supratemporal fossa. The broken line on the right side of the key diagram shows the course of the sensory canals.

greater than it is in *Caproberyx*. Most of the surface of the frontal, particularly the posterior part and the supraorbital flange, is strongly ornamented with small tubercles and sinuous ridges: this ornament resembles that in *Caproberyx superbus* rather than the large straight ridges on the frontals of living holocentrids. The supraorbital sensory canal passed on to the frontal from the sphenotic, gave off a short branch into a depression on the posterior part of the supraorbital flange, and then entered the bone through an elongated pore. Within the bone the canal gave off two posterior branches which passed back in tubes to the hind end of the frontal, the more medial of these branches leading into the depression and grooves on the parietal. The sensory canal gave off a medial branch opening into a narrow median channel between the frontals, similar in size and position to the median mucus cavity in *Caproberyx superbus*, but partially roofed by raised flanges of bone. Passing forwards within the frontal, the sensory canal gave off a lateral branch through a much elongated pore, covered above by a flange of bone, leading to a groove above the anterior part of the orbit. From a pore in the anterior end of the frontal the canal passed into the nasal. The nasals (*na.*), which were attached to the frontals by connective tissue, not by suture, are small, tubular bones, ornamented with ridges and tubercles. Between the nasals the large " V "-shaped dorsal part of the mesethmoid (*mes.*) is exposed. There is no trace of an antorbital in any specimen : the bone was probably absent, as it is in *Caproberyx*. In the roof of the orbit of the holotype and 105736 an orbitosphenoid (*ors.*, Text-fig. 8) is visible, similar in size and shape to that of *Caproberyx superbus* but apparently without the lateral fenestra present in the latter ; in living holocentrids the orbitosphenoid is much reduced in comparison with these Cretaceous forms. As is usual in these small, crushed fishes from the Lebanon, no details of the basicranium are visible in any specimen. The parasphenoid is straight, with lateral flanges articulating with the endopterygoids. The vomer is not visible in any specimen. The lateral ethmoids (*l. e.*) are deep and well ossified.

Infraorbital series. The infraorbital series consists of the usual five bones. The two posterior infraorbitals are small and slender with coarsely serrated posterior edges and a smooth flange covering the groove for the sensory canal. The first and second infraorbitals are longer and a little deeper, with the edge of the flange over the sensory canal serrated and coarse ridges on the ventral part of the bone. There is a

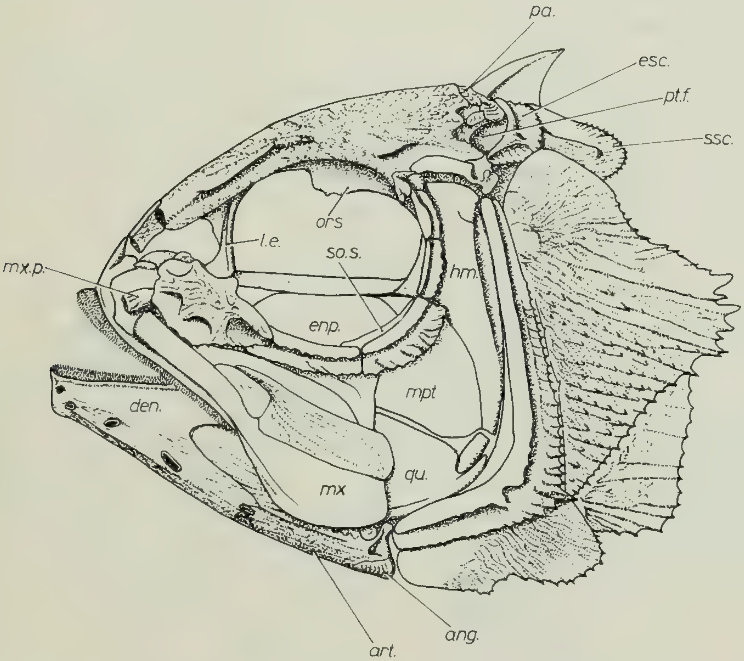

FIG. 8. *Stichocentrus liratus* gen. et sp. nov. Restoration of the skull in left lateral view, ×3·5 approx. *ang.*, angular ; *art.*, articular ; *den.*, dentary ; *enp.*, endopterygoid ; *esc.*, extrascapular ; *hm.*, hyomandibular ; *l.e.*, lateral ethmoid ; *mpt.*, metapterygoid ; *mx.*, maxilla ; *mx.p.*, maxillary process of palatine ; *ors.*, orbitosphenoid ; *pa.*, parietal ; *pt.f.*, post-temporal fossa ; *qu.*, quadrate ; *so.s.*, subocular shelf ; *ssc.*, suprascapular.

subocular shelf (*so. s.*) on the second, third and fourth infraorbitals, but not apparently on the first, although the shelf on the second infraorbital extends forwards some way along the medial face of the first. The lachrymal is deeper than the infraorbitals but does not extend back below the first infraorbital as it does in *Caproberyx* (Text-fig. 10). The groove for the sensory canal on the lachrymal is covered for most of its length by a broad bridge of ornamented bone, with two large pores in its ventral part. Dorsally the lachrymal articulated with the lateral ethmoid by a broad facet. As noted above, there is no antorbital.

Palate and jaws. The hyomandibular (*hm.*) has a broad, undivided head, and is inclined backwards a little. The symplectic inclines forwards at about 35° to the hyomandibular so that the condyle of the quadrate (*qu.*) lies below the posterior part of the orbit. The ectopterygoid and palatine are toothed but the endopterygoid (*enp.*) is toothless. The large maxillary process of the palatine (*mx. p.*) fits in a broad groove on the dorsal surface of the maxilla.

The premaxilla has a low ascending process, which is only a little over a quarter of the length of the toothed alveolar process and is hardly longer than the articular process of the bone. The toothed border of the premaxilla becomes broader and projects a little anteriorly, but the anterior teeth are not enlarged as they are in *Holocentrus* and *Myripristis*. The maxilla (*mx.*) is more than two-thirds as long again as the premaxilla and is expanded behind the latter, but is without teeth. The posterior expansion of the maxilla has a few weak ridges near the ventral margin. There are two supramaxillae, the posterior with a process overlapping the anterior. The posterior supramaxilla is strongly ornamented with longitudinal ridges. The anterior supramaxilla is rather large, extending forwards well beyond the tip of the process on the posterior bone, and is ornamented with a few very weak ridges.

The mandible is long, and moderately deep. The coronoid process of the dentary bears teeth to its tip ; the band of teeth does not become much broader at the symphysis and the teeth are not enlarged there. The ventral parts of the dentary (*den.*) and articular (*art.*) are ornamented with strong longitudinal ridges. There is a small angular (*ang.*) at the back of the jaw. The mandibular sensory canal ran in a tube, closed in the articular but with five pores in the dentary, two at the symphysis, two equally spaced along the bone, and one at the suture with the articular.

Opercular bones. The preopercular is long and strongly angulated, with its vertical limb inclined backwards a little. The posterior edge of the bone bears ridges ending in serrations which grow stronger towards the angle, where one is enlarged into a small spine. The edge of the flange covering the groove for the sensory canal is smooth except near the angle, where there are a few weak, blunt serrations and a single narrow bridge over the groove.

The opercular is large and strongly ornamented. Radiating from the point of suspension of the bone there are sinuous, bifurcating ridges and on the ventral two-thirds of the bone there is also a series of strong, parallel, spiny ridges, each ending in a coarse serration on the edge of the bone. Opposite the point of suspension there are five or six spines on the edge of the bone, with weaker serrations above them. The ornament of the opercular is very like that in *Hoplopteryx simus*, a trachichthyid from the English Chalk (Smith Woodward, 1902, pl. 8, fig. 2). On the antero-dorsal corner of the opercular there are two or three small scales. The ornament of the subopercular is similar, with parallel ridges ending in serrations, interspersed with weaker, sinuous ridges. The large interopercular has coarse, sinuous ridges on the ventral two-thirds of its surface, and serrations on its ventral edge. In the centre of the edge of the interopercular there is an excavation : a similar excavation occurs in the living *Holocentrus*, but there it is covered by the much enlarged preopercular spine.

Hyoid arch and branchiostegals. The ceratohyal is very deep and is perforated by a large, oval fenestra : it resembles that of *Caproberyx* (Patterson, 1964, text-fig. 73) rather than the shallow, unperforated ceratohyals of living holocentrids. There are eight branchiostegals, the four anterior rays articulating with the medial face of the ceratohyal, the four posterior ones with the lateral face of the bone. There is a large, rectangular urohyal.

Vertebral column. There are 26 vertebrae, eleven abdominal and fifteen caudal. All the abdominal vertebrae except the first bear ribs, which are inserted on transverse processes on the last three. There appear to be no epipleurals. The caudal skeleton will be described in detail in a forthcoming work, but it agrees with that of *Holocentrus* (Gosline, 1961 : 14) in having a neural crest on the second pre-ural centrum and the second ural centrum fused with the fused first pre-ural and ural centra, although the line of fusion is clearly visible and the caudal skeleton appears more " upturned " than in living holocentrids. The neural and haemal spines of the first three pre-ural vertebrae are expanded, as they are in living holocentrids.

Pectoral and pelvic girdles and fins. The pectoral girdle contains the normal berycoid complement of bones. The extrascapular (*esc.*) has serrations on its

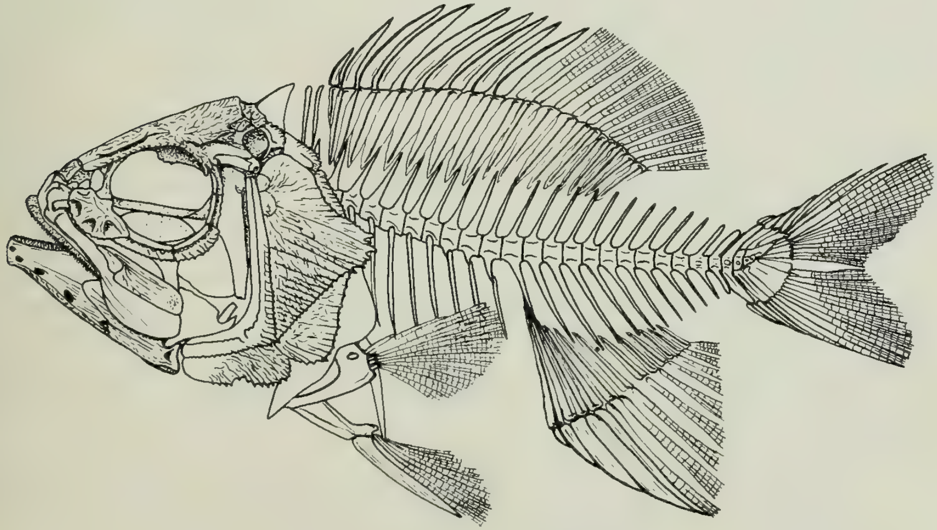

FIG. 9. *Stichocentrus liratus* gen. et sp. nov. Restoration of the skeleton, scales omitted, × 1·7 approx.

posterior edge, ridges ending in serrations on its ventral edge, and a ridge over the groove for the sensory canal in the centre of the bone. On the suprascapular (*ssc.*) the sensory canal ran forwards in a groove covered by a vertical flange of bone ; this flange is ornamented with ridges, and on the edges of the posterior half of the bone there are ridges ending in serrations. The supracleithrum bears similar ridges and serrations. The posterior plate of the cleithrum bears only a few sinuous ridges. The anterior process of the coracoid is long and stout, arching forwards to the tip of the cleithrum. The four pectoral radials are the usual small, hourglass-shaped bones, increasing in size downwards. The large pectoral fin contains ten rays, the third of which is the longest.

The pelvic fins are thoracic, the pelvic bones making contact with the cleithra and the fins being inserted well in front of the tip of the ventral postcleithrum. The pelvic fin contains a very stout, ridged spine, equal in length to the longest anal spine, and seven soft rays.

Median fins. The dorsal fin arises close behind the head, in advance of the pectorals, and occupies most of the back of the fish. The fin contains nine spines and eleven soft rays ; the spines are stout, gently curved, and almost smooth. The first four spines increase in length, the fifth and sixth are equal in length and the last three decrease in length very slightly. The spines are alternately inclined to right and left, as they are in living holocentrids, so that in the fossils they appear to be alternately thick and thin (Pl. 3). In the holotype (64 mm. standard length), on which Text-fig. 9 is mainly based, the longest dorsal spines are equal in length to a little less than the distance between the base of the spines and the vertebral column, but in some of the smaller specimens, particularly 105987 (42 mm. standard length), the spines are longer, equal in length to about half the maximum depth of the trunk. The available material suggests that this difference is not taxonomically significant, but that the length of the dorsal spines was variable in the species and that during ontogeny the depth of the trunk increased in proportion to the length of the dorsal spines.

The first radial of the dorsal fin is not enlarged, and is inserted between the second and third neural spines. The fin is preceded by two predorsals lying between the first and second neural spines. The spine-bearing dorsal radials are expanded, meeting each other in slightly dentate sutures.

The anal fin originates below the middle of the soft dorsal and contains five spines, the first of which is extremely small, and nine soft rays. The spines increase in length from front to rear and are weakly ridged and very stout. The fifth spine, although longer than the fourth, is more slender, as in *Myripristis* (where there are only four spines). The longest anal spine is rather variable in length : it is longer than the longest dorsal spine in the holotype, about equal to the longest dorsal spine in 105736 and 108929, and shorter than the longest dorsal spine in 108923. The first anal radial is not much enlarged.

The forked caudal fin contains nineteen principal rays with seventeen branched (nine in the upper lobe, eight in the lower). The principal rays are preceded by four small spines and one segmented ray above and below.

Squamation. The scales are thick, large and coarsely ctenoid. The exposed area of each scale is ornamented with weak ridges and tubercles passing back to the ctenii on the hind edge. There are twelve scales in a transverse series on the trunk, with the lateral line passing through the fifth scale from the top, and about twenty-six scales along the lateral line. Scales cover the cheek and there are one or two scales on the antero-dorsal corner of the opercular. The scales overlap the bases of the dorsal and anal fins, both soft and spinous portions, as they do in living holocentrids. Between the pelvic and anal fins there is a median series of ridge scales, not enlarged or much thickened, as in *Caproberyx.*

AFFINITIES. As has been emphasized in the comparisons made in the description above, *Stichocentrus* is a holocentrid berycoid. Falling in the suborder Berycoidei because of its toothless endopterygoid, pelvic spine and nineteen-rayed caudal, it is allied with the Holocentridae rather than the Trachichthyidae by the nine dorsal spines (no more than eight in any trachichthyid), the seven soft rays in the pelvics, the absence of crests and large mucus cavities on the skull roof, the posterior extension of the frontals and the small supratemporal fossa, the large mesethmoid, the rather shallow infraorbitals with a subocular shelf on the last three, and the enlarged penultimate anal spine.

Three other genera of Cretaceous holocentrids are known : *Caproberyx* (Lower Cenomanian of Morocco, Middle Cenomanian of Hakel (p. 98) and Turonian of England), *Trachichthyoides* (Upper Cenomanian of England) and *Kansius* (Lower Senonian of Kansas). *Trachichthyoides* is known only by a single head (Smith Woodward, 1902, pl. 8, fig. 5 ; Patterson, 1964 : 359). It differs from *Stichocentrus* in having the mucus cavities on the skull roof larger and the ornamented areas and supraoccipital crest smaller, in the deeper, more strongly ornamented infraorbitals, with the lachrymal extending back below the first infraorbital, and in the shorter jaws, with the suspensorium inclined forwards. But the general features of the two skull roofs and the form and ornament of the opercular bones are very similar and in *Trachichthyoides* there is no subocular shelf on the first infraorbital, just as in *Stichocentrus.*

From *Kansius,* in which only the trunk is known (Hussakof, 1929), *Stichocentrus* differs in having one or two fewer dorsal fin spines, with a less marked decrease in length in the posterior spines, and in having the last anal spine longer than the penultimate. But in size, in the proportions of the trunk and the size and position of the fins the two genera are very similar.

In *Caproberyx* (Patterson, 1964 : 341, 416 ; p. 98) the skull roof resembles that of *Stichocentrus* more closely than any other known form, but in *Stichocentrus* the supraoccipital crest and supratemporal fossa are smaller and the frontals extend back farther. *Caproberyx* also differs from *Stichocentrus* in having only six or seven dorsal fin spines, with the last the longest, in having more soft rays in the anal fin, in the posterior extension of the lachrymal below the first infraorbital, the subocular shelf on the first infraorbital, the shorter, more strongly expanded maxilla, etc., but again there are many similarities between the two genera.

The five anal spines of *Stichocentrus* are a peculiar feature. No living holocentrid has more than four, and although five spines have been described in *Kansius*

(Hussakof, 1929 : 3) Conrad (1941 : 17) has given reasons for doubting that there were more than four, an interpretation which seems to be confirmed by Hussakof's description of the enlarged third spine as having two spines behind it, a feature known in no other holocentrid. In *Caproberyx superbus*, which has been described as having only four spines (Smith Woodward, 1902 : 12 ; Patterson, 1964 : 357) a complete series of spines is not well preserved in any specimen, but some individuals, particularly in P.9153, appear to have had a very small anterior spine making a total of five, as in *Stichocentrus*.

Recent workers (Conrad, 1941 ; Nelson, 1955 ; Dunkle & Olsen, 1959) recognize two subfamilies in the Tertiary and recent holocentrids, the Holocentrinae, containing among living genera *Holocentrus* and *Plectrypops* according to Conrad (1941), *Holocentrus* alone according to Nelson (1955), and the Myripristinae, containing *Myripristis*, *Ostichthys*, *Holotrachys*, *Plectrypops* and *Corniger* according to Nelson (1955). These subfamilies are differentiated by characters such as the form of the otic bulla, the spine on the preopercular, the elongated nasals and premaxillary ascending processes, short jaws and deep spiny lachrymal of *Holocentrus*. Among Cretaceous holocentrids, *Trachichthyoides* is allied to the myripristine line in characters of the skull roof, lachrymal and preopercular, while *Caproberyx* resembles the holocentrines in the skull roof and the deep lachrymal. *Kansius* is insufficiently known to be confidently placed in either subfamily. *Stichocentrus* resembles *Caproberyx* and the holocentrines in its skull roof and infraorbitals, but is closer than *Caproberyx* to the living holocentrids in the nine dorsal fin spines, alternately inclined to left and right and with the last four decreasing in length, and in the enlarged penultimate anal spine. Thus among the four known genera of Cretaceous holocentrids one can see the gradual acquisition of such Recent holocentrid features as the form of the dorsal and anal fins (in the sequence *Caproberyx–Stichocentrus–Kansius*), the posterior extension of the frontals and the reduction of the supratemporal fossa and supraoccipital crest (in the sequence *Caproberyx–Stichocentrus*), the development of a subocular shelf on all the infraorbitals (in the sequence *Trachichthyoides–Stichocentrus–Caproberyx*). But all these Cretaceous genera (so far as they are known) differ from the Tertiary and living holocentrids in a number of characters such as the absence of an antorbital, the simple, tubular nasals, the large pores along the course of the mandibular sensory canal (in living holocentrids the mandibular sensory canal is almost entirely enclosed), the presence of scales only on the antero-dorsal corner of the opercular (in living holocentrids scales cover the whole anterior part of the opercular), the deep, perforate ceratohyal and the occasional presence of five anal spines. Some of these characters are certainly primitive, but others such as the absence of an antorbital and maxillary teeth and the five anal spines are specialized and seem to exclude the known Cretaceous holocentrids from the direct ancestry of later members of the family. Certainly the Cretaceous holocentrids are more closely related to each other than they are to the Tertiary and living genera, and they cannot reasonably be included in either of the subfamilies recognized among living forms (these subfamilies seem merely to emphasize the specializations of *Holocentrus* itself). At present the evidence suggests that the Holocentridae underwent two radiations, one in the Cretaceous and one in the Tertiary, the Tertiary forms being derived from ancestors as yet unknown. In the Cretaceous radiation the fins and skull roof gradually acquired features approaching those of modern forms, but there remain considerable differences between the two groups. I propose that the Cretaceous forms be included in a new subfamily Caproberycinae, defined as follows : Holocentridae in which the dorsal fin is undivided, with 6–11 spines, anal with 4–5 spines, the penultimate sometimes enlarged, nasals simple and tubular, no antorbital, no maxillary teeth, large pores along the course of the mandibular sensory canal, otic bulla as in *Myripristis* where known, no preopercular spine, only two or three scales on the antero-dorsal corner of the opercular, ceratohyal deep and perforate.

One other species must be mentioned in discussing *Stichocentrus*. This is *Hoplopteryx lewisi* (Davis), under which name the specimens of *Stichocentrus* in Beirut were catalogued by Smith Woodward (in *ms*.). *Stichocentrus liratus* and *Hoplopteryx lewisi* are distinguished by the occurrence of the first only at Hajula, the second only at Hakel, and by the presence in *H. lewisi* of only 22–23 vertebrae (not 22–24 as I stated : Patterson, 1964 : 406), a long premaxilla, an unexpanded maxilla, a large supratemporal fossa extending well forward over the orbit, the penultimate anal spine not enlarged, etc. But in size, shape and proportions of the trunk, number and structure of the fin spines and the shape and ornamentation of the superficial bones of the head the two species are strikingly similar. Further, in P.8689 and P.10709 (*H. lewisi*) there are traces of at least one large scale on the antero-dorsal part of the opercular, a difference from all other trachichthyids except *Lissoberyx* (p. 77) and a resemblance to *Stichocentrus*. This tends to confirm that the scaleless opercular of trachichthyids is secondarily derived from a scaly opercular (p. 107). The strong similarity between *Stichocentrus liratus* and *Hoplopteryx lewisi* provides further evidence of the close relationship between the Holocentridae and Trachichthyidae in the Cretaceous : in the English Chalk a similar comparison may be made between *Hoplopteryx lewesiensis* and *Caproberyx superbus*, but here we know that the similarities extend to habitat as well as habitus, for in B.M. (N.H.) 33486 two large individuals, one of *C. superbus* and one of *H. lewesiensis*, are preserved side by side in the same block of Chalk.

Genus ***CAPROBERYX*** Tate Regan, 1911 : 8

DIAGNOSIS. See Patterson (1964 : 341), but add " lachrymal extending back below first infraorbital, dorsal fin with six or seven spines, dorsal spines not alternately inclined to right and left, scales moderately large, about 12–15 in each transverse series ".

TYPE SPECIES. *Beryx superbus* Dixon (1850) (= *Berycopsis major* Smith Woodward) from the Turonian zones of the English Chalk.

Caproberyx pharsus sp. nov.

(Pl. 4, fig. 2 ; Text-fig. 10)

DIAGNOSIS. A *Caproberyx* known only by a specimen lacking the posterior half of the trunk ; probably about 6·25 cm. in standard length ; length of head slightly less (93%) than maximum depth of trunk, the latter probably equal to about 45% of the standard length ; skull roof without ornament except for a few ridges on the parietal, the supraorbital flange and near the median mucus cavity, which is partially roofed, as in *Stichocentrus* ; infraorbitals with serrated edges, otherwise smooth, posterior infraorbitals not tubular ; hind margins of preopercular and opercular coarsely serrated, operculum with weak radiating ridges ; dorsal fin with six spines, pelvic apparently with only six soft rays ; scales thick on antero-ventral part of trunk, thin elsewhere, 15 or 16 scales in a transverse series.

HOLOTYPE. B.M. (N.H.) P.47836 (Pl. 4, fig. 2), a fish lacking the posterior half of the trunk, part of the head in counterpart. The only specimen.

HORIZON AND LOCALITY. Middle Cenomanian ; Hakel, Lebanon.

DESCRIPTION. Since this species is known only by a single incomplete and rather poorly preserved specimen the description which follows is incomplete, and the assignment to *Caproberyx* must be regarded as provisional. The specimen has been prepared by transfer in a resin block.

Measurements and proportions. The length of the preserved part of the fish (to the second caudal vertebra) is 40 mm. ; the standard length is estimated to have been about 6·25 cm. The length of the head is 26 mm., the maximum depth of the trunk 28 mm. The species was thus rather deep-bodied, the depth of the trunk being greater than the length of the head and equal to about 45% of the standard length, compared with about 40% in the other known species of *Caproberyx.*

Neurocranium. The skull roof is shown in Text-fig. 10. There is a high, triangular supraoccipital crest (*soc.*), thickened anteriorly, which is larger than that of *Stichocentrus* (Text-fig. 7) but smaller than in *C. superbus* (Patterson, 1964, text-fig. 67). The supratemporal fossa was clearly short and broad, as in *Stichocentrus* and *C. superbus*, but detailed comparisons are not possible. The parietals (*pa.*) are poorly preserved, but near the mid-line they bore an area of fine ridged and tubercular ornament. Laterally, the parietal extends ventrally in the wall of the post-temporal fossa ; while it is impossible to be certain how much of this wall was formed by the parietal it appears that there was a broad contact, not covered by the frontal, between the parietal and the pterotic (*pto.*) in the wall of the fossa. This is a primitive feature which does not occur in *Caproberyx superbus* or *Stichocentrus*, but is present in *Trachichthyoides* and *Lissoberyx* (Text-fig. 2) and is indicated in Arambourg's figure (1954, text-fig. 68) of the skull roof of *Caproberyx polydesmus.* The frontal appears to extend as far postero-laterally as it does in *C. superbus* but not so far as in *Stichocentrus* and in general the posterior part of the skull roof seems closest to that of *Caproberyx* but with a more complete roof to the post-temporal fossa. The frontals (*l. fr.*, *r. fr.*) are much less strongly ornamented than they are in *Caproberyx* and *Stichocentrus*, the only ornament consisting of a few weak ridges on the flange which roofs the median mucus cavity (see below) and a series of short ridges on the supraorbital flange of the bone.

The main cephalic sensory canal, passing on to the pterotic from the extrascapular, ran forwards in an open groove, covered laterally by a raised flange, with the preopercular sensory canal passing ventrally behind this flange in the usual way.

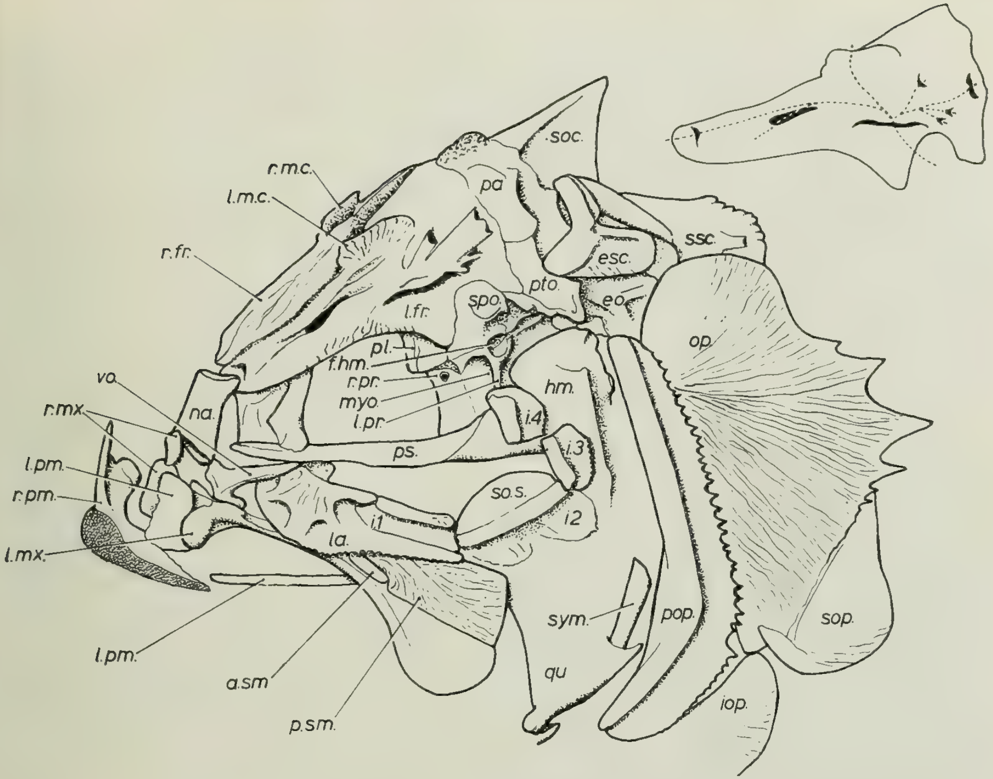

FIG. 10. *Caproberyx pharsus* sp. nov. The head of the holotype as preserved, some bones partially restored from the counterpart, ×5 approx. Inset at top right is a diagram of the left frontal showing the course of the supraorbital sensory canal. *a.sm.*, anterior supramaxilla; *eo.*, exoccipital; *esc.*, extrascapular; *f.hm.*, articular facet for hyomandibular; *hm.*, hyomandibular; *i.*1, *i.*2, *i.*3, *i.*4, infraorbitals 1–4; *iop.*, interopercular; *la.*, lachrymal; *l.fr.*, left frontal; *l.m.c.*, roof of median mucus cavity on left frontal; *l.mx.*, left maxilla; *l.pm.*, fragment of head and alveolar process of left premaxilla; *l.pr.*, left prootic; *myo.*, myodome; *na.*, left nasal; *op.*, opercular; *pa.*, parietal; *pl.*, left pleurosphenoid; *pop.*, preopercular; *ps.*, parasphenoid; *p.sm.*, posterior supramaxilla; *pto.*, pterotic; *qu.*, quadrate; *r.fr.*, right frontal, crushed and displaced; *r.m.c.*, roof of median mucus cavity on right frontal; *r.mx.*, head of right maxilla; *r.pm.*, right premaxilla; *r.pr.*, right prootic; *so.s.*, subocular shelf on second infraorbital; *soc.*, supraoccipital crest; *sop.*, subopercular; *spo.*, left sphenotic, its orbital margin bent upwards; *ssc.*, suprascapular; *sym.*, symplectic; *vo.*, vomer.

Passing over the surface of the sphenotic (where there was presumably an anastomosis with the infraorbital canal), the supraorbital canal ran antero-dorsally on to the frontal and entered a horizontal tube in the bone through a much elongated foramen (inset, Text-fig. 10). There is no sign in *C. pharsus* of the depression on the supraorbital flange of the frontal which in *C. superbus* and *Stichocentrus* received a branch given off from the canal before it entered the bone: the great elongation in *C. pharsus* of the foramen through which the canal entered the bone suggests that this branch was given off within the opening, approaching the condition in living holocentrids where the branch is given off after the canal has entered the tube in the bone. In the tube in the frontal the canal gave off the usual posterior branch, which in *C. pharsus* was subdivided into four (compared with two in *C. superbus* and *Stichocentrus*), one large branch passing back in a tube to the hind end of the frontal, a smaller and shorter branch in a tube above this and two still smaller and shorter ones below it (inset, Text-fig. 10). The medial branch of the supraorbital canal passed into an elongated median mucus cavity, similar in size and position to that of *C. superbus* but partially roofed by a raised, ornamented flange of bone (*l.m.c.*, *r.m.c.*), as in *Stichocentrus* (Text-fig. 7). After giving off the median branch, the supraorbital canal passed forwards within the frontal to its anterior end, giving off a lateral branch through an elongated pore above the anterior half of the orbit.

Only the left nasal (*na.*) is preserved, a moderately large, trapezoid bone, without ornament and apparently tubular, enclosing a broad passage for the sensory canal, as in *Stichocentrus*.

The vomer (*vo.*) is preserved but displaced, and it is impossible to see whether it bore teeth. The parasphenoid (*ps.*) is straight and toothless, as is normal in holocentrids. The anterior parts of the prootics are visible (*l. pr.*, *r. pr.*), showing nothing to distinguish them from the prootics of *C. superbus*. A wide myodome (*myo.*) opens between the prootics. The elongated facet for the hyomandibular (*f. hm.*) is formed by the prootic, sphenotic and pterotic, in the usual way, and there is a large dilatator fossa in the sphenotic and pterotic above this facet. No basisphenoid is preserved. The pleurosphenoid (*pl.*) appears to be larger than in *C. superbus* and shows the usual groove for the superficial ophthalmic nerves. Traces of an orbitosphenoid are preserved, but the shape of the bone cannot be made out.

Infraorbital series. The infraorbital series contains the usual five bones. The lachrymal (*la.*) resembles that of *Caproberyx superbus* (Patterson, 1964, text-fig. 70) in depth and in the long postero-ventral process extending back below the first infraorbital to touch the second ; as in *C. superbus* there is a broad bridge over the groove for the sensory canal, with large pores near the ventral margin, but the surface of the bone is almost smooth. The ventral edge of the lachrymal is serrated. The first infraorbital (*i.* 1) is shallow and unornamented except for a few ridges on the posterior part of the flange over the sensory canal. The second, third and fourth infraorbitals (*i.* 2–4) are all deeper than the corresponding bones in *C. superbus* and much deeper than those of *Stichocentrus* ; they have a smooth flange over the groove for the sensory canal and serrated ventral edges. The second infraorbital, incomplete ventrally, has a broad groove in its centre marking a branch of the sensory canal. There is a very broad subocular shelf (*so. s.*) on the second infraorbital, but whether the shelf was present on all the infraorbitals as in *C. superbus* and living holocentrids cannot be seen.

Palate and jaws. The hyomandibular (*hm.*) has a broad, undivided head and a very broad proximal part, as in *C. superbus*. The hyomandibular is inclined backwards a little, with the symplectic (*sym.*) and quadrate (*qu.*) inclined forwards so that the quadrate condyle lies below the posterior edge of the orbit. The endopterygoid is toothless but the anterior part of the ectopterygoid is toothed. The palatine is not visible.

The premaxilla (*r. pm.*) has a rather high ascending process, probably equal in length to about one-third of the toothed alveolar process (although the latter is not completely preserved). As in *Stichocentrus*, the tooth patch on the premaxilla becomes broader anteriorly, but there are no enlarged teeth. The maxilla (*l. mx.*) is about 40% longer than the premaxilla, as in *C. superbus*, proportionately much shorter than in *Stichocentrus*. The maxilla is expanded behind the premaxilla and is without ornament or teeth. There are two supramaxillae, the posterior one (*p. sm.*) ornamented with ridges radiating from a longitudinal ridge in the centre of the bone, the anterior (*a. sm.*) almost smooth. The posterior supramaxilla bears the usual process overlying the anterior.

Of the mandible almost nothing is preserved. The bones were clearly only feebly ornamented.

Opercular series and branchiostegals. The preopercular (*pop.*) is bent through about 50°, compared with 60° in *C. superbus* and *Stichocentrus*. The dorsal limb of the preopercular is inclined backwards a little. The broad flange covering the groove for the sensory canal is smooth, as in *C. superbus*, and does not form a bridge at the angle in the bone as it does in *Stichocentrus*. The hind edge of the preopercular is strongly and coarsely serrated but there is no enlarged spine at the angle in the bone.

The posterior edge of the opercular (*op.*) is produced into spines, with a large one opposite the point of suspension and a larger one just below, as in *C. polydesmus* (Arambourg) but not in *C. superbus*. The ornament of the opercular, weak ridges radiating from the point of suspension, resembles that in *C. superbus* and is quite unlike that in *Stichocentrus*. There are two or three scales on the antero-dorsal corner of the opercular, as is usual in Cretaceous holocentrids. The subopercular (*sop.*) and interopercular (*iop.*) are poorly preserved but appear to have been of normal form, the interopercular with ridges near its ventral edge, the subopercular with a few ridges, possibly ending in weak serrations, at its antero-ventral margin.

The hyoid arch and branchiostegals are very imperfectly preserved : most of the branchiostegals are missing and their number cannot be estimated.

Vertebral column. Only the first thirteen vertebrae are preserved. There are eleven abdominal vertebrae, the last four with transverse processes on which the ribs are inserted. Whether there are ribs on the second centrum, as there are in *Stichocentrus* and *Lissoberyx*, cannot be seen. Epipleural bones are visible articulating with the centra of the last three abdominal vertebrae.

Pectoral and pelvic girdles and fins. The extrascapular (*esc.*) is similar in shape to that of *C. superbus*, with a short, broad ventral limb and a longer, more slender dorsal limb, but has a smooth posterior edge and only a few weak ridges on the ventral limb. The suprascapular (*ssc.*) has a moderately long dorsal limb and a very broad posterior plate, with a coarsely serrated hind margin. The supracleithrum appears to be less broad than that of *C. superbus* and has coarse serrations on the upper part of its posterior edge. The posterior plate of the cleithrum is smooth. Of the endoskeletal pectoral girdle nothing can be seen. The ventral postcleithrum reaches the ventral border of the trunk well behind the origin of the pelvic fin and the pelvic girdle was in contact with the cleithra. The pectoral fin contains about eleven rays and is rather small, its length being only about one-quarter of the maximum depth of the trunk. The pelvic fin contains a stout, weakly ribbed spine, equal in length to a little more than one-third of the maximum depth of the trunk, and apparently only six soft rays, a difference from *C. superbus* and all other holocentrids which is possibly due only to imperfect preservation, although the fin appears to be complete.

Median fins. Of the median fins, only the anterior part of the dorsal fin is preserved. This contains six smooth spines, increasing in length from front to rear, and nine soft rays : there were probably two or three more soft rays. The spines are not alternately inclined to left and right as they are in *Stichocentrus* and living holocentrids. The longest spine, the sixth, is equal in length to about 40% of the maximum depth of the trunk. The first dorsal radial, supporting the first and second spines, is inserted between the third and fourth neural spines. Preceding the dorsal fin there are three predorsals, one lying in front of each of the first three neural spines.

Squamation. The scales on the antero-ventral part of the trunk are thick and coarsely ctenoid ; on the rest of the trunk the scales are much thinner and though their hind margins are nowhere perfectly preserved they appear to be feebly ctenoid. On the trunk there were fifteen or sixteen scales in each transverse series, with the lateral line passing through the tenth or eleventh scale above the ventral border. It is not possible to see whether ventral ridge scales were present. The lateral line scales are not enlarged or thickened. Scales cover the cheek, the postero-lateral parts of the skull roof and the antero-dorsal corner of the opercular.

AFFINITIES. Although this species is known only by a single poorly preserved and very incomplete specimen it shows some points of interest. The specimen is shown to be a member of the Berycoidei by the combination of an orbitosphenoid, two supramaxillae, a pelvic with a spine and six soft rays, and dorsal fin spines. Within the Berycoidei the form of the skull roof, with a small supratemporal fossa, a largely enclosed supraorbital sensory canal with only a small median mucus cavity, and various other resemblances to the Cretaceous holocentrids *Caproberyx* and *Stichocentrus*, show it to be a member of the Holocentridae. The specimen differs from all other Holocentridae in having only six dorsal fin spines, with the sixth the longest, but in this it is close to *Caproberyx*, in both species of which (*C. superbus* (Dixon) and *C. polydesmus* (Arambourg)) there are seven dorsal spines. Among other resemblances to *Caproberyx* the most striking is the form of the infraorbitals, with the lachrymal sending back a long process along the entire length of the first infraorbital (the lachrymal is similar in *Trachichthyoides*). Less important resemblances to *Caproberyx* include the form of the posterior part of the skull roof (see p. 98), the proportions of the maxilla and premaxilla, the opercular ornament and the presence of epipleurals. All these characters are in contrast with *Stichocentrus*, but there are others in which the specimen resembles *Stichocentrus* and differs from *Caproberyx*. These include the roofed median mucus cavity and the simple, non-tubular posterior infraorbitals. Apart from these characters shared with either *Caproberyx* or *Stichocentrus*, the skull roof and superficial bones of the skull in general are less strongly ornamented than they are in any other holocentrid, living or fossil, the posterior branch of the infraorbital sensory canal is more complex than it is in *Caproberyx* and *Stichocentrus*, there is an extensive contact between the parietal and pterotic in the wall of the post-temporal fossa, a character otherwise known in holocentrids only in *Trachichthyoides*, and there are only six soft rays in the pelvic fin, a difference from all other holocentrids and a resemblance to Trachichthyidae. Reviewing these various similarities and differences, I think it possible that the species represents a new genus, resembling *Caproberyx* in many characters, *Stichocentrus* in a few, and being more primitive than either in others. But I am unwilling to erect a new genus on such fragmentary material and pending the discovery of more complete specimens refer the species provisionally to *Caproberyx*.

V. DISCUSSION

There are described in this paper four berycoids, three from Cenomanian beds (Hakel & Hajula) and one from Senonian (Sahel Alma), representing three new genera and possibly four. Apart from increasing the number of known Cretaceous berycoid genera by 50% these new forms show certain features bearing on the origin and evolution of the Berycoidei.

(*i*) *Distinction between families in Cretaceous Berycoidei*

All known Cretaceous Berycoidei can be placed in either the Trachichthyidae (*Hoplopteryx, Acrogaster, Tubantia, Lissoberyx, Gnathoberyx*) or the Holocentridae (*Caproberyx, Trachichthyoides, Kansius, Stichocentrus*). But as has been shown above (pp. 80, 97) separation of these families becomes increasingly difficult as more Cretaceous forms are described. This is borne out by a list of the characters in which the two families are held to differ in the most recent diagnoses (Patterson, 1964 : 304, 341) :

(i) In Trachichthyidae there are fewer dorsal spines. But in the holocentrid *Caproberyx* the number of dorsal spines falls to 6–7, less than in many living and some fossil trachichthyids ; and in *Caproberyx* the spines are not inclined alternately to left and right as they are in most holocentrids.

(ii) The pelvic fins have six soft rays in Trachichthyidae, seven in Holocentridae. But in the holocentrid *Caproberyx pharsus* (p. 102) there appear to be only six soft rays (this conclusion is based only on one specimen, but in it the pelvic fin is well preserved).

(iii) In Trachichthyidae the skull roof bears high crests separating large mucus cavities, in Holocentridae broad ridges separating small mucus cavities. But in the trachichthyid *Lissoberyx* the skull roof is without crests or mucus cavities and has a sensory canal pattern very like that in the holocentrid *Myripristis*.

(iv) In Trachichthyidae the supratemporal fossa is large, in Holocentridae the frontals extend posteriorly and the fossa is small. But in the trachichthyid *Lissoberyx* the supratemporal fossa is of moderate size, intermediate between those of *Hoplopteryx* (Trachichthyidae) and *Caproberyx* (Holocentridae).

(v) In Trachichthyidae the mesethmoid is reduced. But in *Lissoberyx* the mesethmoid is not much reduced and approaches those of holocentrids in size.

(vi) The infraorbitals are deep in Trachichthyidae, shallow in Holocentridae. This difference still holds good for the Cretaceous genera, but in the living holocentrids *Plectrypops* and *Holotrachys* the infraorbitals are deeper than the lachrymal, just as they are in most trachichthyids.

(vii) The subocular shelf extends along all the infraorbitals in Holocentridae but is confined to the second infraorbital in Trachichthyidae. This difference still seems to hold good, although there is no subocular shelf on the first infraorbital in the holocentrids *Stichocentrus* and *Trachichthyoides*.

(viii) In Trachichthyidae the gape is large and the maxilla is not much expanded posteriorly, in Holocentridae the gape is smaller and the maxilla is expanded. But in the trachichthyids *Lissoberyx* and, in particular, *Gnathoberyx* there is no significant difference from holocentrids.

(ix) In Holocentridae there are scales on the anterior part of the opercular, in Trachichthyidae the opercular is without scales. But in the trachichthyid *Hoplopteryx lewisi* there is at least one large scale on the antero-dorsal part of the opercular, and in *Lissoberyx* the opercular is almost completely scaled.

Some of the features which differentiate living members of the Trachichthyidae and Holocentridae are already known to fail in Cretaceous genera (two supramaxillae in Holocentridae, one in Trachichthyidae ; antorbital present in Holocentridae, absent in Trachichthyidae ; ventral ridge scales present in Trachichthyidae, absent in Holocentridae : see Patterson, 1964), but the new forms described here show that almost all the differences between the two families no longer hold good. From a purely taxonomic point of view the exceptions listed above make it very difficult to provide adequate diagnoses of the two families, but since there is rarely any difficulty in deciding to which of the families any particular form belongs (see p. 80) there is little point in modifying the familial diagnoses by listing exceptions to every character. From a more general standpoint the Cretaceous Berycoidei give an excellent and well documented picture of the early evolution of a group. Today the Trachichthyidae and Holocentridae are well separated, moderately successful groups, the first containing bathypelagic fishes of wide distribution, the second neritic fishes of the tropics and sub-tropics. The trachichthyids also seem to be the stem group of a number of bathypelagic (Melamphaeidae, Stephanoberycidae, Gibberichthyidae, Korsogasteridae, Berycidae, Anoplogasteridae, Diretmidae) and neritic (Monocentridae, Anomalopidae) families, some of which were already differentiated in the Eocene (Berycidae, Monocentridae ; Casier, 1966), others in the Miocene (Melamphaeidae, Ebeling, 1962), but most of which are without fossil record. The Trachichthyidae and Holocentridae can both be traced back to the Cenomanian, but in the Upper Cretaceous the two families converge strongly, with a blurring of the distinctions between them. This shows that in the Upper Cretaceous the " trachichthyid " and " holocentrid " facies had not yet become fully established, the Cretaceous fauna consisting of forms showing " experimental " combinations of characters. Simpson (1953 : 340–349) gives an excellent account of similar cases, mainly in mammals, and rightly comments on the difficulties of attempts to cram the early, diverging members of phyletic lines into higher categories (in this case families) based on what these lines are later to become.

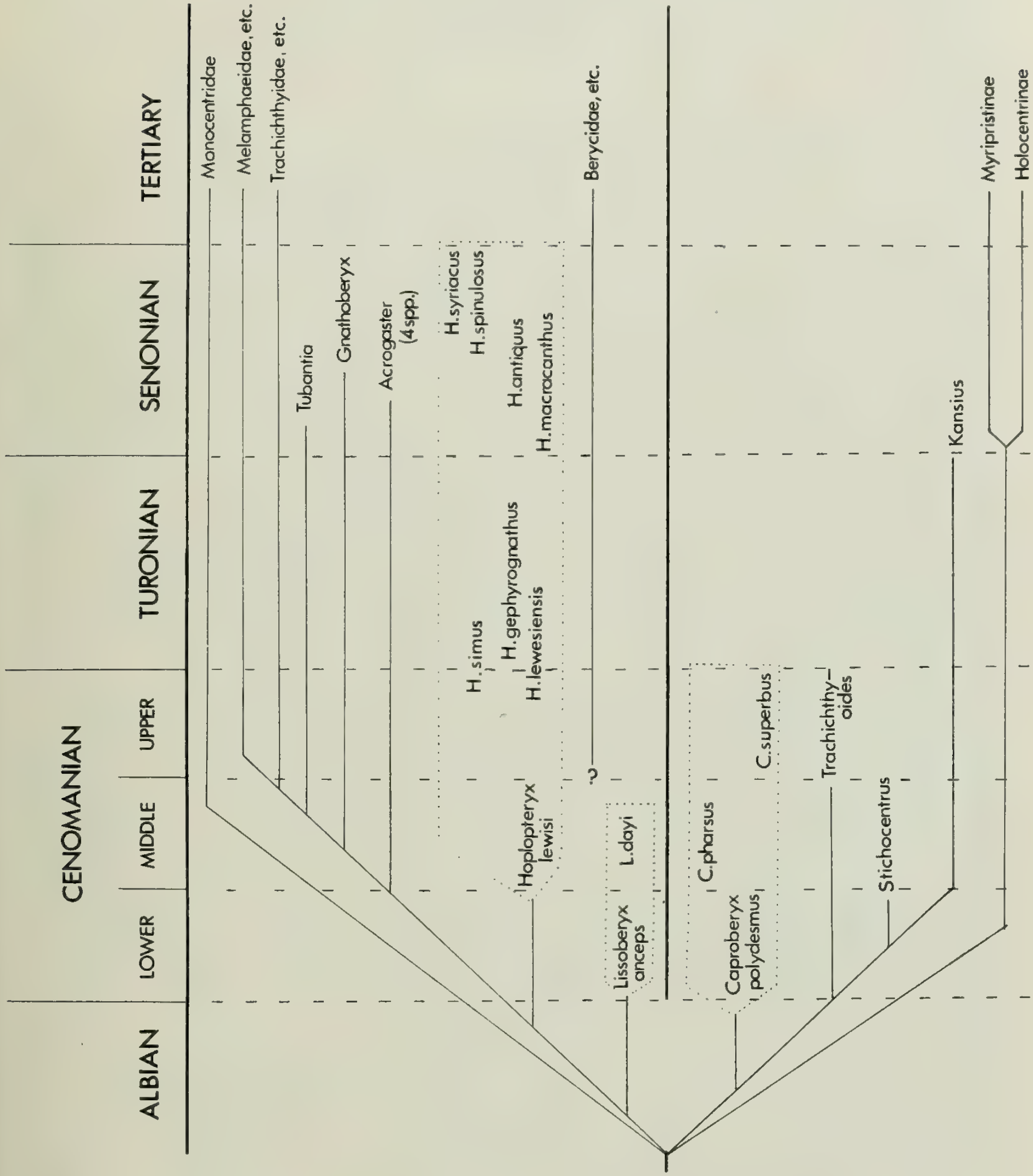
TERTIARY
SENONIAN
TURONIAN
CENOMANIAN
UPPER
MIDDLE
LOWER
ALBIAN
Monocentridae
Melamphaeidae, etc.
Trachichthyidae, etc.
Tubantia
Gnathoberyx
Acrogaster (4 spp.)
H. syriacus
H. spinulosus
H. antiquus
H. macracanthus
H. simus
H. gephyrognathus
H. lewesiensis
Hoplopteryx lewisi
Bercidae, etc.
?
Lissoberyx anceps
L. dayi
Caproberyx polydesmus
C. pharsus
C. superbus
Trachichthyoides
Stichocentrus
Kansius
Myripristinae
Holocentrinae

FIG. 11. A diagram suggesting the probable interrelationships of the known Cretaceous Trachichthyidae (left) and Holocentridae (right) and the living families of Berycoidei. Distance from the central, vertical line indicates degree of divergence from the common ancestor of the Berycoidei.

My present opinion of the interrelationships of the known Cretaceous Berycoidei is summarized in Text-fig. 11. General features worth noting in the early history of this suborder are the mosaic nature of the character combinations in the early forms and the fact that no genus seems to provide an entirely adequate ancestor for any later genus.

(*ii*) *The Origin of the Berycoidei*

We have seen that in the Cenomanian the Berycoidei were a group of recent origin in which much variation occurred. These early berycoids also exhibit a number of primitive characters which are absent or rare in Tertiary and living berycoids, including a toothed maxilla (*Gnathoberyx, Hoplopteryx macracanthus, Myripristis*) a partially roofed post-temporal fossa (*Hoplopteryx, Lissoberyx, Trachichthyoides, Caproberyx pharsus*) and an antorbital (*Hoplopteryx*, living holocentrids). In particular, *Lissoberyx* is a form which must lie very close to the origin of the suborder, sharing many characters of Trachichthyidae and Holocentridae. The primitive features of *Lissoberyx* have some bearing on the origin of the order Beryciformes as a whole, a question which I have discussed at some length (Patterson, 1964 : 459). I thought then that the Beryciformes might be diphyletic, the Berycoidei having an origin independent of the other two suborders, because I could see no convergence towards a common type between the two main suborders, Polymixioidei and Berycoidei, as they were traced back towards their first appearance in the Cenomanian, although there is good evidence of convergence towards a basal type within each suborder. While this is still true of the major characters separating the two suborders (caudal formula and presence or absence of a pelvic spine, epineurals and endopterygoid teeth), *Lissoberyx* is a berycoid which tends towards the polymixioids in the absence of ornament on the bones of the head, the smooth skull roof without mucus cavities, the high supraoccipital crest (all characters which I have used in separating the two suborders : Patterson, 1964 : 433), and in the completely scaled opercular. In all these characters *Lissoberyx* also resembles the four monotypic Cretaceous families placed in the suborder Dinopterygoidei (Patterson, 1964 : 434). The structure of *Lissoberyx* therefore increases the possibility that the Beryciformes is a monophyletic order and suggests that the ancestral form would have been a small fish with a smooth skull roof, a high supraoccipital crest arising from a moderately large supratemporal fossa, no ornament on the bones of the head, a reduced antorbital, a toothed maxilla, a scaly operculum and a partial roof to the post-temporal fossa. Only the last of these points excludes the Ctenothrissiformes from the direct ancestry of the group.

One or two other points in the anatomy of the Cretaceous Berycoidei are worth discussing briefly. All known Cretaceous Beryciformes, both polymixioids and berycoids, have a very constant sensory canal pattern on the skull roof : the main features of this pattern are a well developed parietal branch of the supraorbital canal extending back to open at the hind end of the frontal, usually into a depression on the parietal, this branch often being subdivided (into five branches in *Berycopsis* and *Homonotichthys*, four in *Caproberyx pharsus*, etc.), a medial branch meeting its fellow in a median depression over the orbit, and a lateral branch over the anterior part of the orbit. This pattern of the supraorbital canal seems to be very widely distributed among primitive teleosts, although Gosline, Marshall & Mead (1966 : 3) find that the medial branches fail to meet in a cross-commissure in " isospondylous " fishes. An exactly similar pattern occurs in the Ctenothrissiformes, except that in *Aulolepis* the parietal branch is reduced and does not reach the parietal. A well developed parietal branch of the supraorbital canal, terminating in or near the parietal, is generally held to be a relic of the posterior part of the supraorbital canal and the anterior pit-line of halecostomes and more primitive actinopterygians. Arambourg (1950 ; 1954 : 34, 72) considers that such parietal branches occur only in the most primitive teleosts (*Clupavus*, *Thrissopater*) but my own observations suggest that they are more widely distributed, although it is doubtful whether the parietal branches are strictly primary or even homologous in all teleosts.

The subocular shelf has been shown by Smith & Bailey (1962) to be an important taxonomic feature. Among living teleosts a subocular shelf occurs only in the Acanthopterygii (*sensu* Greenwood *et al.*, 1966) and in the osteoglossiform family Notopteridae (Greenwood *et al.*, 1966 : 363), where it is undoubtedly developed independently. There is also a subocular shelf in all the Cretaceous Beryciformes. Otherwise, a subocular shelf is only known to occur in the Cretaceous ctenothrissiform *Ctenothrissa* (Patterson, 1964 : 229), where there is a narrow shelf on the first and anterior part of the second infraorbitals. This is powerful additional evidence for close relationship between the Ctenothrissiformes and the ancestral Beryciformes.

The presence of scales on the opercular is undoubtedly an advanced character in actinopterygians since scales could not develop over the dermal opercular until it had lost its covering of enameloid tissue, which can develop only in contact with the ectoderm. The opercular is without scales in all elopomorph, clupeomorph and osteoglossomorph teleosts, and in protacanthopterygian teleosts opercular scales are only present below the myctophoid level in esocoids and alepocephaloids. In Beryciformes the occurrence of a completely scaled opercular in Cretaceous and living polymixioids, in dinopterygoids and in *Lissoberyx* strongly suggests that this feature is primitive for the order, and presumably for all acanthopterygians. This hypothesis receives support from the completely scaled operculars of the Ctenothrissiformes *Aulolepis*, *Pateroperca* and the Lebanese species of *Ctenothrissa*. In Berycoidei scales are absent on the opercular in all Trachichthyidae except *Lissoberyx* and *Hoplopteryx lewisi* while in Holocentridae the opercular is only scaled anteriorly. These are clearly cases of secondary reduction from a complete scale covering, evidently associated with the development of spiny ornament on the opercular. An analogous situation occurs in the Ctenothrissiformes, where *Ctenothrissa microcephala* and *C. radians* show progressive reduction in the scaling of the opercular associated with increased ornamentation.

A common ancestor of the three suborders of Beryciformes, all of which are present and clearly distinct in the Cenomanian, must have lived in the Albian or earlier. It is worth briefly reviewing the few records of supposed Beryciformes in pre-Cenomanian beds. Weiler (1947) referred to the Berycomorphi isolated scales and a pelvic fin from the Upper Aptian of Armenkov Island, S. Georgia. These specimens have not been figured and the scales, which were very briefly described, are evidently without clearly diagnostic features. The pelvic fin is described as containing a short, slender spine, one unbranched soft ray and six branched rays. These specimens seem doubtful evidence of Beryciformes in the Aptian. Much earlier in time, beryciform otoliths have been described from the Tithonian and Wealden of Germany (Martin & Weiler, 1954, 1957). These Jurassic and Wealden otoliths must be treated with some reserve : since otoliths can at present only be identified by comparison with living forms the accuracy of otolith determinations must decrease with increasing age.

In the Gault of S.E. England (at Small Dole, near Henfield, Sussex, Ford Place, Wrotham, Kent, and King's Lynn, Norfolk) there occur fragmentary remains of two small teleosts, one with ctenoid scales bearing parallel rows of small, flat spines which resemble those of *Ctenothrissa* and some berycoids, the other with scales in which the exposed circuli are broken up into very small tubercles. As yet, I have seen no fin spines or other structures diagnostic of Beryciformes with these fragments, but various skull bones are very suggestive of the Ctenothrissiformes and Beryciformes. The first of these small teleosts appears to have a toothed maxilla and two very small patches of teeth on the endopterygoid : the second has a broad, cavernous premaxilla of typical trachichthyid type. Since fragments of these small fishes are not uncommon at certain horizons in the Middle Gault it may eventually prove possible to give an account of Beryciformes in the Middle Albian.

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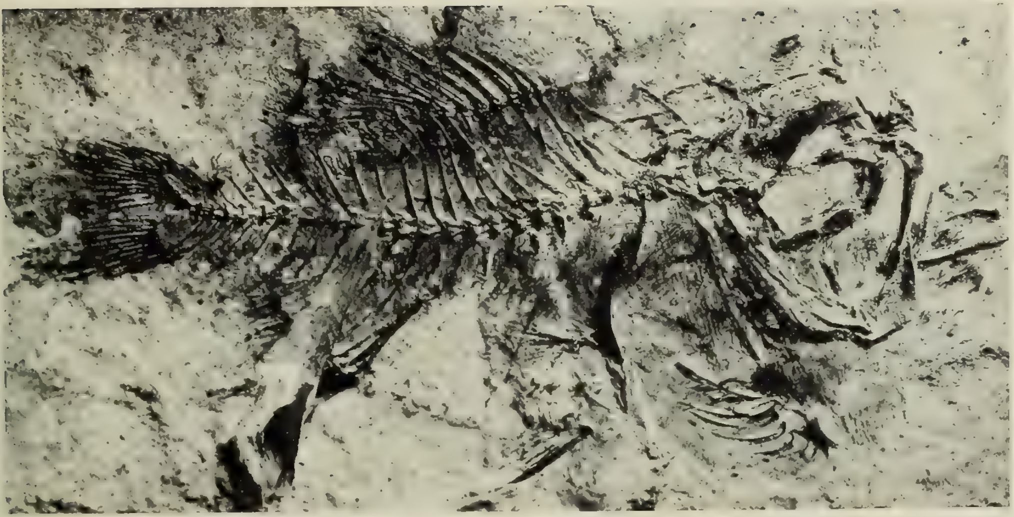
PLATE 1

Fig. 1. ***Lissoberyx dayi*** (Smith Woodward). AUB 108926, Hajula, Lebanon, prepared by transfer in a resin block. × 3·5.

Fig. 2. ***Gnathoberyx stigmosus*** gen. et sp. nov. The holotype, AUB 100402, Sahel Alma, Lebanon, before preparation of the upper jaw. × 3.

PLATE 1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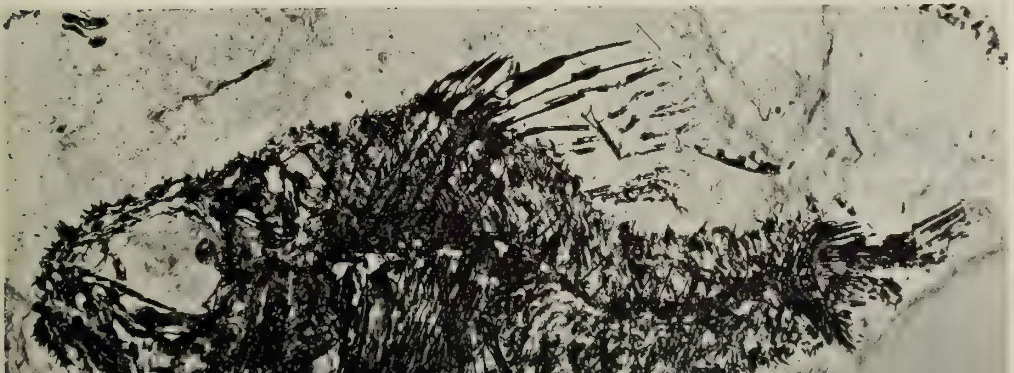
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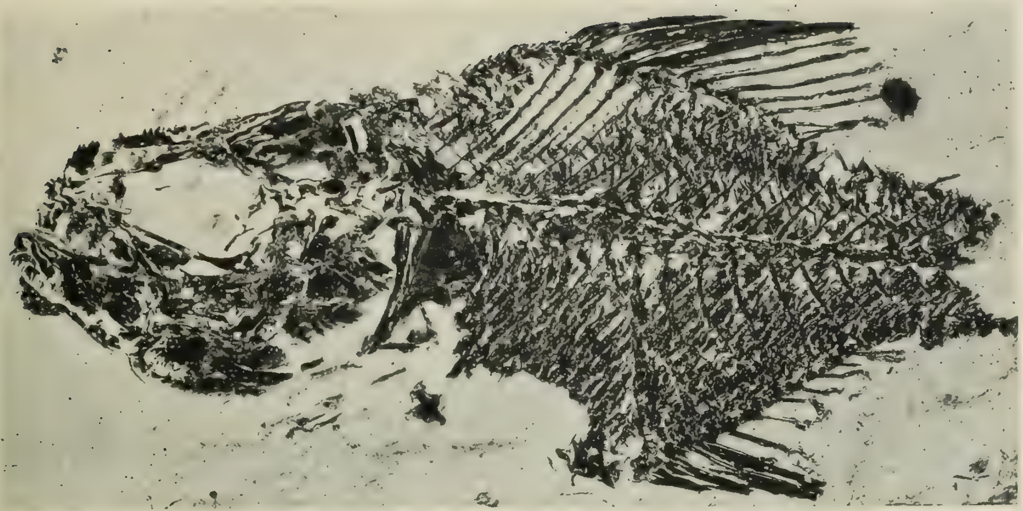
PLATE 2

Gnathoberyx stigmosus gen. et sp. nov., Sahel Alma, Lebanon.

FIG. 1. AUB 103838, × 3·25.

FIG. 2. The head of the holotype, AUB 100402, after preparation to show the toothed maxilla and premaxilla. × 10.



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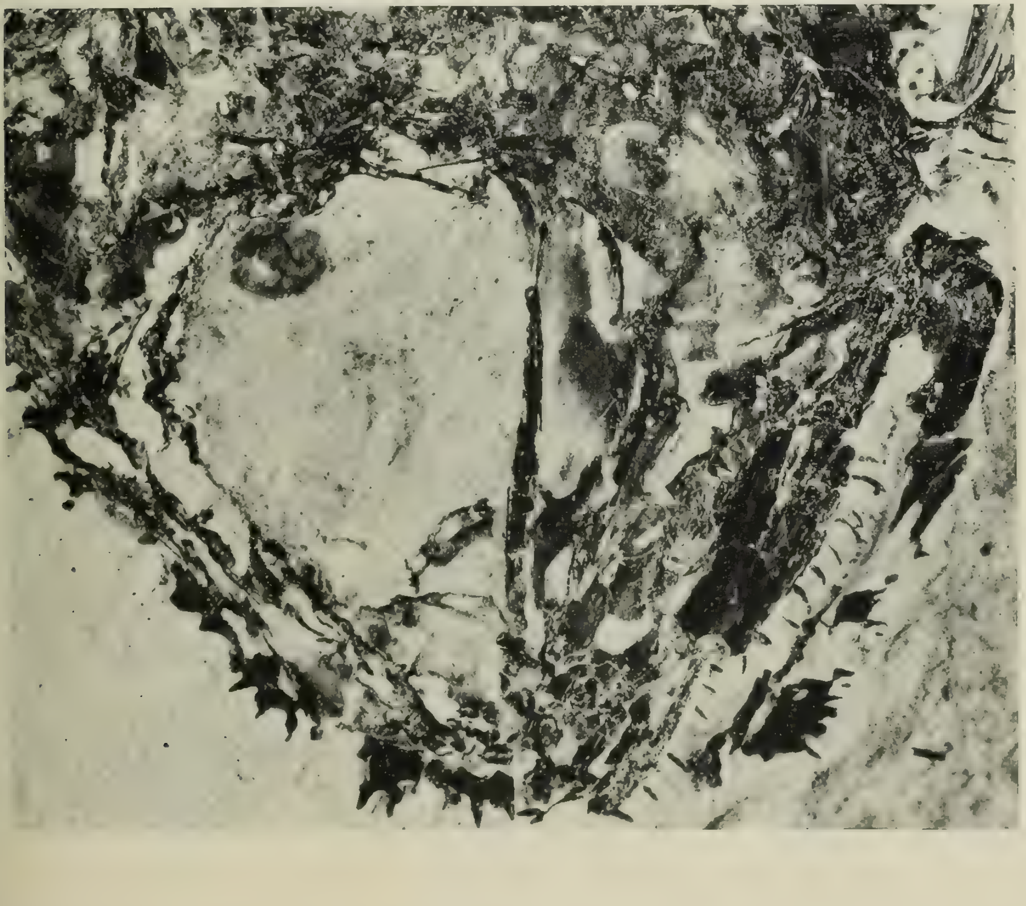

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PLATE 3

Stichocentrus liratus gen. et sp. nov. The holotype, B.M. (N.H.) P.47835, Hajula, Lebanon prepared by transfer in a resin block. × 3.

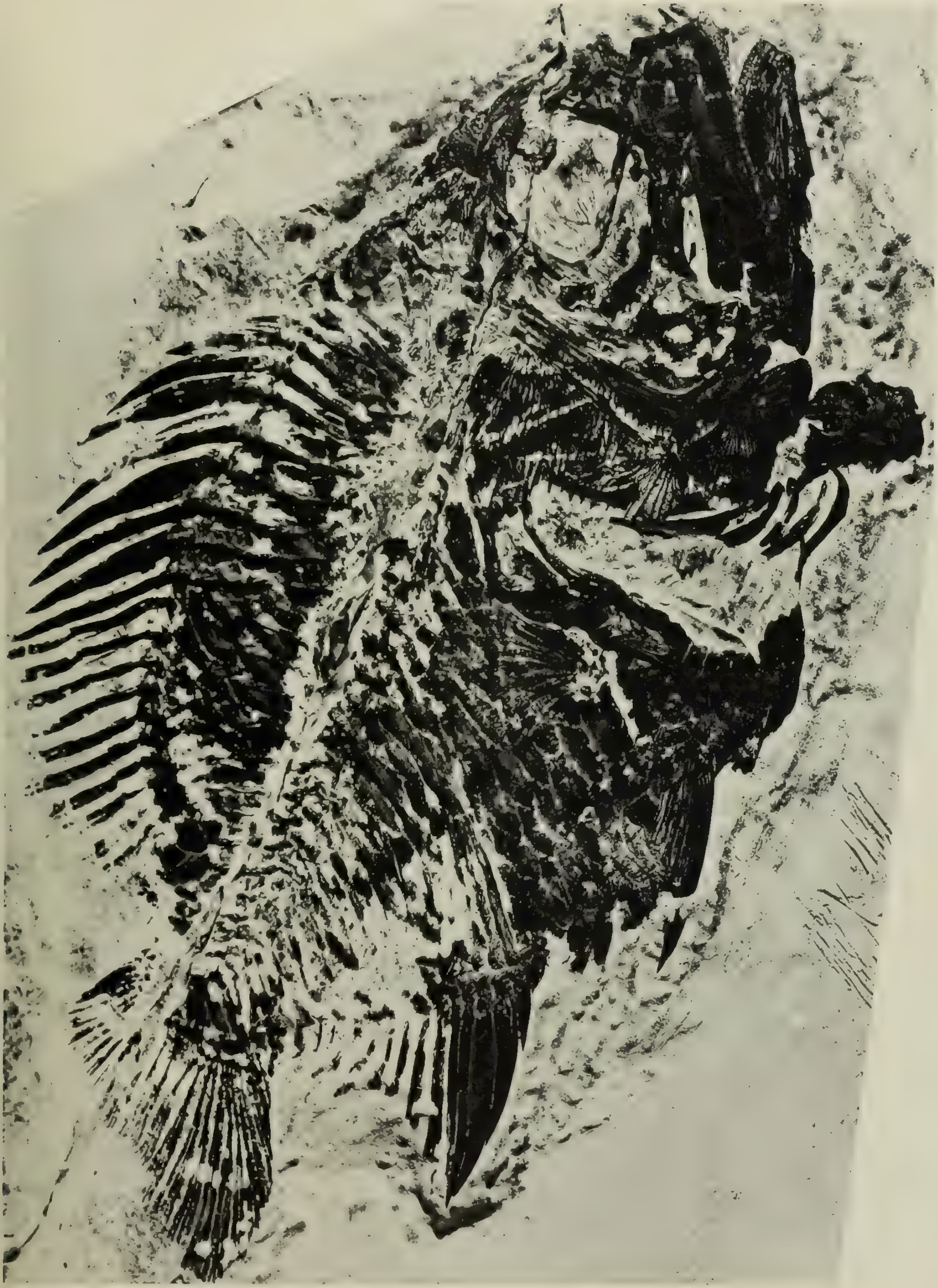
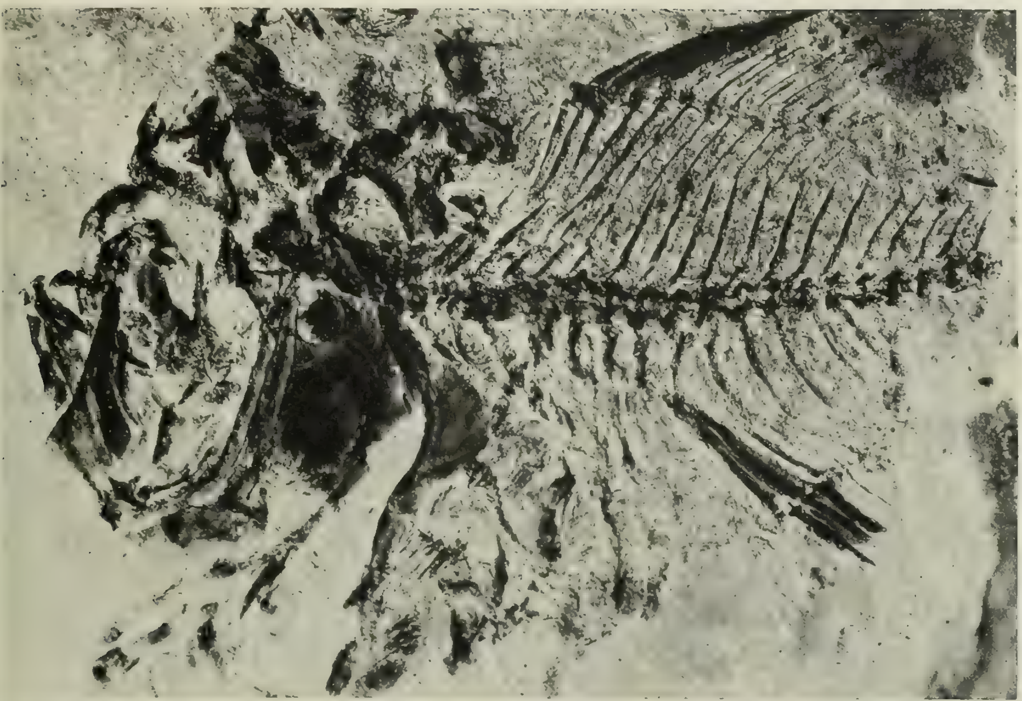


PLATE 4

Fig. 1. ***Lissoberyx dayi*** (Smith Woodward). AUB 107578, Hakel, Lebanon, prepared by transfer in a resin block. × 5·5.

Fig. 2. ***Caproberyx pharsus*** sp. nov. The holotype, B.M. (N.H.) P.47836. Hakel, Lebanon. prepared by transfer in a resin block. × 2·85.



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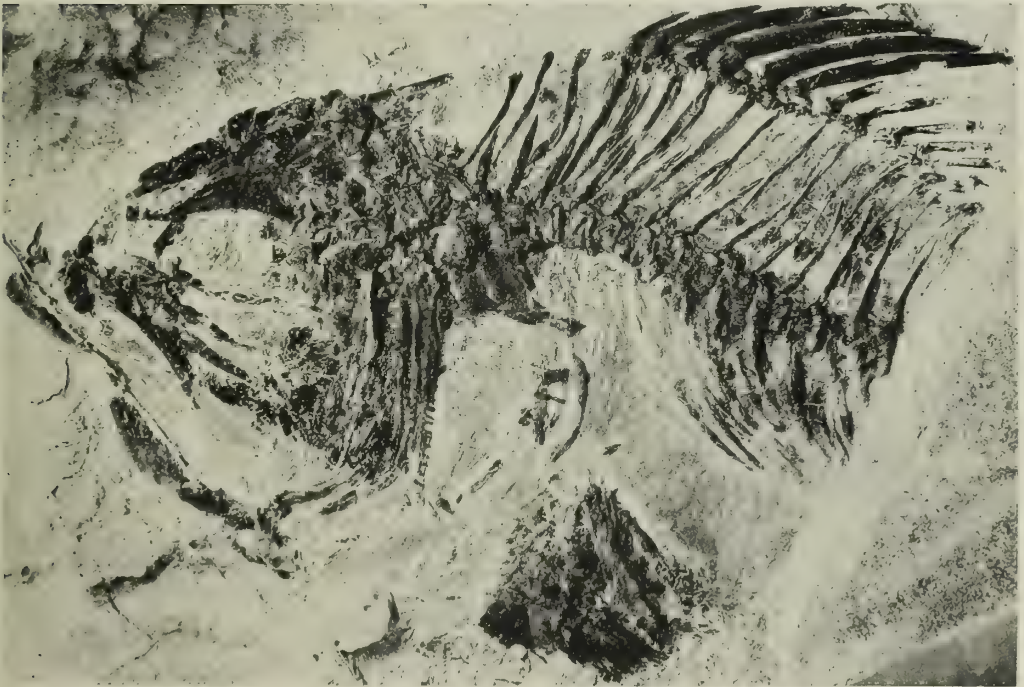

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STRATIGRAPHY AND PALAEOGEOGRAPHY OF THE YORKSHIRE OOLITES AND THEIR RELATIONSHIPS WITH THE LINCOLNSHIRE LIMESTONE

R. H. BATE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 14 No. 4
LONDON: 1967

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BY

RAYMOND HOLMES BATE

Pp. 111–141 ; 5 *Text-figures* ; 4 *Tables*

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STRATIGRAPHY AND PALAEOGEOGRAPHY OF THE YORKSHIRE OOLITES AND THEIR RELATIONSHIPS WITH THE LINCOLNSHIRE LIMESTONE

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SYNOPSIS

The Lincolnshire Limestone is correlated stratigraphically and on its ostracod fauna with the Hydraulic Limestone/Eller Beck Bed horizon and the Cave, Whitwell and Millepore Oolites and associated Upper Limestone and Yons Nab Beds of Yorkshire. The stratigraphy of these beds is discussed. The Hydraulic Limestone and the Eller Beck Bed are identified as facies variants of the same marine transgression correlated with the Lower Lincolnshire Limestone. The Cave, Whitwell and Millepore Oolites, the Upper Limestone and the Yons Nab Beds are correlated with the Upper Lincolnshire Limestone. The highest beds of the Upper Lincolnshire Limestone are older than the Grey Limestone Series of Yorkshire which is not represented in Lincolnshire. Eleven geological sections are described in detail and the palaeogeography of the marine horizons is discussed.

I INTRODUCTION

IN previous publications (Bate 1963, 1963*a*, 1964) I have dealt with the ostracod faunas of the Lower Lincolnshire Limestone, the Cave Oolite and underlying marl and of the Whitwell and Millepore Oolites of Yorkshire. This study involved a stratigraphical investigation of the beds in question and it is now possible to show how the oolites, geographically isolated one from the other, were laid down contemporaneously in a shallow sea which covered north-eastern England at that time.

The dating of the Yorkshire and Lincolnshire Oolites is rather tenuous at the present time, and all that can be satisfactorily stated is that they are Bajocian, with part of the period of deposition taking place during *Hyperlioceras discites* times.

The purpose of the present paper is to give detailed sections, complete with the ostracod faunas found therein, and to use these faunas to correlate the Lincolnshire Limestone and the Yorkshire Oolites and at the same time to suggest the probable palaeogeography at that time.

In order to retain uniformity throughout related publications on the Middle Jurassic of north-eastern England I have retained the stratigraphical names used

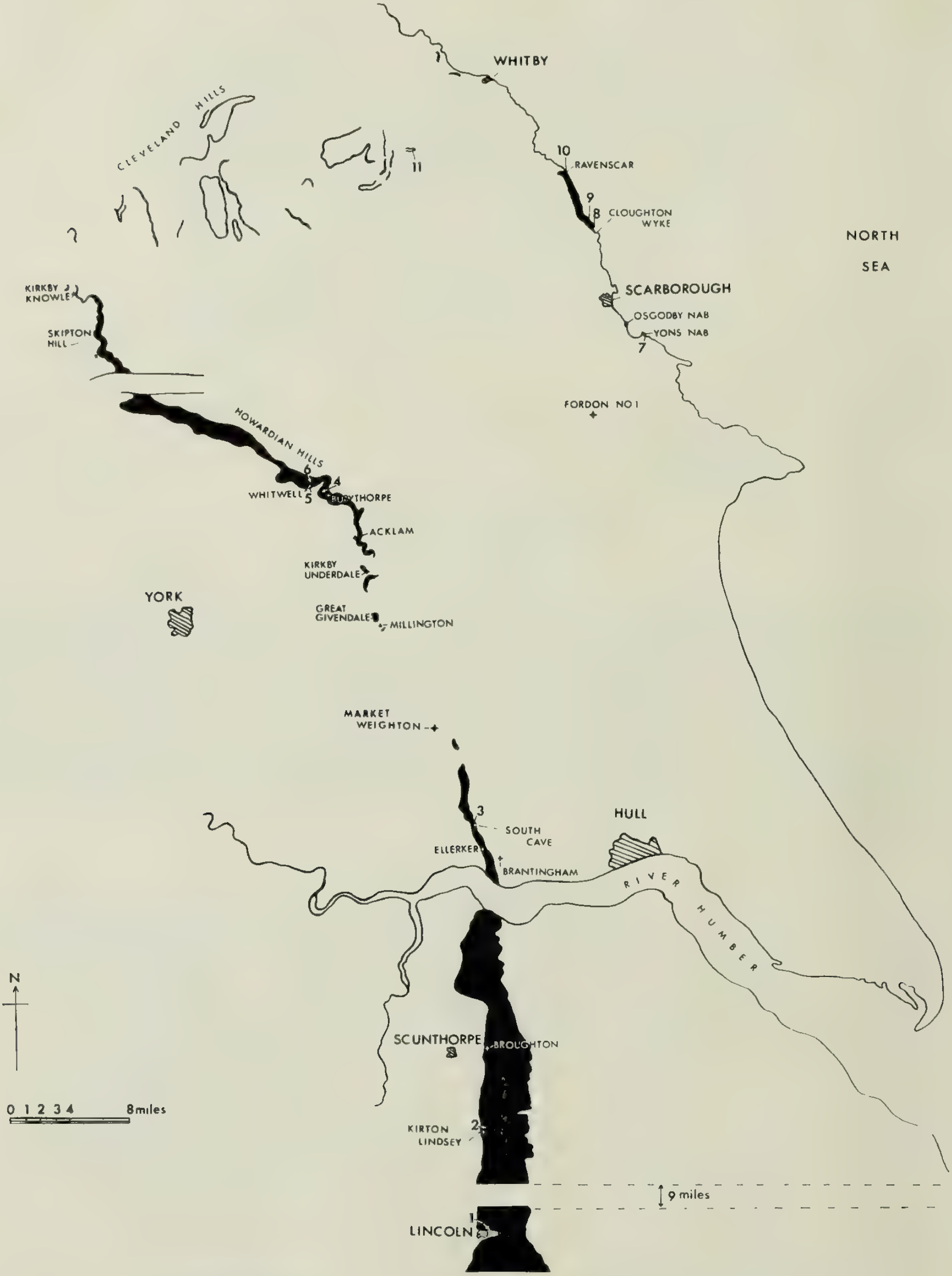

WHITBY
CLEVELAND HILLS
11
10
RAVENSCAR
9
8
CLOUGHTON WYKE
NORTH SEA
KIRKBY KNOWLE
SKIPTON HILL
SCARBOROUGH
OSGODBY NAB
YONS NAB
7
FORDON NO 1
HOWARDIAN HILLS
6
4
WHITWELL
5
BURYTHORPE
ACKLAM
KIRKBY UNDERDALE
YORK
GREAT GIVENDALE
MILLINGTON
MARKET WEIGHTON
3
SOUTH CAVE
HULL
ELLERKER
BRANTINGHAM
RIVER HUMBER
N
SCUNTHORPE
BROUGHTON
0 1 2 3 4 8miles
KIRTON LINDSEY
2
9 miles
1
LINCOLN

FIG. 1. Map showing localities, sections and outcrop of the Lincolnshire Limestone south of the Humber, and of the correlated marine horizons in Yorkshire. Isolated outcrops in the north-central part of the map belong to the Eller Beck Bed.

previously. By international agreement the term Series is to be restricted to the primary division of a System. The units bearing this term here should not be so regarded.

The localities mentioned throughout the text are indicated in Text-fig. 1, whilst those which have supplied detailed geological sections are listed below with full map references.

1. Lincoln—Greetwell Quarry. Lower Lincolnshire Limestone consisting of the Blue and Silver Beds and the Kirton Cementstone Series, completely exposed. Map reference TF/002725.
2. Kirton Lindsey—Kirton Cement Quarry. Base of the Upper Lincolnshire Limestone, the Kirton Shale (*Acanthothiris crossi* Bed) completely exposed. Map reference SE/942011.
3. South Cave—Eastfield Quarry. Complete exposure of the Cave Oolite and, in 1947, of the underlying marl. Map reference SE/913323.
4. Kirkham—road cutting on the Firby Road. Hydraulic Limestone and underlying marl. Map reference SE/738658.
5. Whitwell—Seamer Lime and Stone Co. Quarry. Almost complete exposure of the Whitwell Oolite and sandy base of the Upper Limestone. Map reference SE/734672.
6. Crambeck—Stonecliff Wood. Top of Whitwell Oolite and almost complete exposure of the Upper Limestone. Map reference SE/737675.
7. Yons Nab headland—Cayton Bay. Complete foreshore section through the Millepore Oolite and Yons Nab Beds. Map reference TA/084844.
8. Cloughton. Complete foreshore section through the Millepore Oolite and Yons Nab Beds. Map reference TA/021958.
9. Hayburn. Complete foreshore section through the Eller Beck Bed. Map reference TA/017964.
10. Ravenscar. Complete cliff section through the Millepore Bed. Map reference NZ/981019.
11. Eller Beck. Almost complete stream section through the Eller Beck Bed. Map reference NZ/833023.

Acknowledgments. The contents of this paper have been based upon part of a Ph.D. thesis submitted to the University of Sheffield in 1961.

II STRATIGRAPHY

North Lincolnshire

The Lincolnshire Limestone

The Lincolnshire Limestone forms a thick lens of limestone striking north–south through Lincolnshire. The facies is variable and in parts (e.g. Ancaster) the limestone is quarried as a valuable building stone. Elsewhere (Kirton Lindsey) it is used in the manufacture of cement.

Although it is intended to make some reference to the Lincolnshire Limestone in the south of the county our main concern is with the outcrop in the north, around Lincoln and Kirton Lindsey. Evans (1952) has written an excellent account of the

BATHONIAN	Blisworth Clay	
	Great Oolite Limestone	
	Upper Estuarine Series	
BAJOCIAN	Upper Lincolnshire Limestone	Hibaldstow Oolite *Acanthothiris crossi* Bed
	Lower Lincolnshire Limestone	Kirton Cementstone Series Blue & Silver Beds
	Lower Estuarine Series Northampton Sand	
LIAS	Upper Lias	

TABLE 1. Succession of Middle Jurassic strata in North Lincolnshire.

Lincolnshire Limestone of this region and this work should be consulted for more detailed information.

The succession in the Lincoln District is as follows (Table 1) :

The base of the Bathonian, the Upper Estuarine Series, overlies the Upper Lincolnshire Limestone unconformably, and so far as the ostracod faunas are concerned bears no relationship to the limestone beneath. A description of the Upper Estuarine Series ostracods is now in the press.

The Lincolnshire Limestone is divisible into Upper and Lower with further subdivisions (in the north) into the Hibaldstow Oolite, the *Acanthothiris crossi* Bed, the Kirton Cementstone Series and the Blue and Silver Beds. Towards the south of Lincolnshire the name Hibaldstow Oolite is changed to the Ancaster Beds. The Lincolnshire Limestone itself lies unconformably on the Lower Estuarine Series beneath. This Series tends to be composed of unfossiliferous sands and clays with occasional plant remains.

According to Swinnerton & Kent (1949) towards the centre of the Lincolnshire Basin the Lincolnshire Limestone is most complete, the highest beds being restricted to the Great Ponton–Ropsley area. The Great Ponton *Terebratula* Beds are the youngest of all. Apart from the *A. crossi* Bed at the base, the Upper Lincolnshire Limestone has generally yielded only a poor ostracod fauna and no detailed sections are given. The ostracods obtained from samples of the uppermost Upper Lincolnshire Limestone are identical with those present lower down. For example the fauna obtained from a large overgrown quarry at Braceby (map reference TF/009351) included the following : *Praeschuleridea subtrigona subtrigona* (Jones & Sherborn), *Aulacocythere punctata* Bate, *Eocytheridea carinata* Bate, *Bairdia hilda* (Jones), *Ektyphocythere triangula* (Brand), *Fuhrbergiella* (*Praefuhrbergiella*) *arens* Bate, *Systenocythere exilofasciata* Bate, *Cytherelloidea catenulata* (Jones & Sherborn) *Pleurocythere kirtonensis* Bate, *Dolocythere maculosa* Bate, *Micropneumatocythere globosa* Bate, *Southcavea reticulata* Bate, *Monoceratina vulsa* (Jones & Sherborn), *Paracypris bajociana* Bate, and *Glyptocythere* sp. Of this fauna only *Glyptocythere* sp. is not present also in the Lower Lincolnshire Limestone, being confined to the highest beds of the Upper Lincolnshire Limestone. This is possibly the lowest occurrence (stratigraphically) of the genus, more typically developed in Yorkshire within the Grey Limestone Series.

The base of the Upper Lincolnshire Limestone is represented by the *A. crossi* Bed which forms a prominent marker across Lincolnshire. In the north at Kirton Lindsey the 14 feet of strata known as the Kirton Shale contain the brachiopod *Acanthothiris crossi* and are regarded here as the lateral equivalent of a much harder limestone bed further south.

The Kirton Cementstone Series of the Lower Lincolnshire Limestone consists of poorly oolitic, rather chalky limestones with marl bands interbedded. The Blue and Silver Beds, on the other hand, tend to be rather more massively bedded and in some cases strongly oolitic. The Lincolnshire Limestone as a whole extends northwards as far as the Humber and is represented on the north bank by the Cave Oolite. Arkell (1933 : 215) correlates this with the Hibaldstow Oolite of Lincolnshire and points out that in a boring at Brantingham the beds below the Cave Oolite are of similar facies to the Kirton Beds. A stratigraphical correlation is therefore possible across the Humber. A few miles further north at South Cave the marine marls below the Cave Oolite were exposed in 1947 in a sump put down in Eastfield Quarry, but as will be seen later do not contain an ostracod fauna completely identical with the Kirton Beds south of the Humber, a number of locally restricted species being present.

South Yorkshire

The Cave Oolite is a shelly oolitic limestone with sand intercalations overlain by approximately 12 feet of sand known as the Upper Estuarine Series. It is doubtful, however, if these sands are of estuarine origin. At the base of the Cave Oolite the brachiopod *Acanthothiris broughensis* Muir-Wood (1952 : 123) is recorded and together with the record of *Acanthothiris crossi* s.l. from the Whitwell Oolite further north has been used to correlate the Whitwell, Cave and Hibaldstow Oolites (Kent, 1955 : 208).

Below the Cave Oolite the marl sequence developed in the region of South Cave forms part of the Basement Beds (Fox-Strangways, 1892 : 176), a name now restricted to the marl beds alone (Neale, 1958 : 164). These marine marls, from 4–6 ft. in thickness, are no longer exposed. The Basement Beds overlie a thin porcellanous limestone known as the Hydraulic Limestone, and Fox-Strangways (1892 : 176) recorded the thickness of this bed in the Market Weighton District as 2 ft. 6 ins. At the present time it does not appear in section, only as fragments on the surface. At Ellerker (map reference SE/927297) a small ostracod fauna comprising the following has been obtained from this bed : *Paracypris bajociana* Bate, *Progonocythere cristata* Bate and *Ektyphocythere triangula* (Brand).

The Lower Estuarine Series, although no longer exposed around Market Weighton (not sampled), is reported to consist of clays and yellow sandy shales with plant remains, shells and crustaceans (Neale 1958 : 164).

The Cave Oolite and the underlying beds extend from the Humber to Market Weighton where they pass beneath the overstepping Chalk.

Much has been written concerning the geological implications of the break in outcrop which occurs at Market Weighton, admirably reviewed by Kent (1955). The ideas put forward have varied from Fox-Strangways' interpretation (1892) that the Market Weighton area was a land barrier extending from the west, to that of Kendall's (1905) that it was an anticlinal feature, a continuation of the Wharfe Axis. Kent's interpretation (1955) was that the Market Weighton area was more in the nature of a broad non-subsiding rigid block.

Jurassic sediments from Rhaetic times onwards were affected by the structure and thin appreciably towards it from both north and south. During the period of deposition with which we are concerned in this paper, it is doubtful whether there was continuous deposition over the structure north–south but rather continuation was effected around the structure to the east. The interpretation that the Market Weighton area was a stable region during Middle Jurassic times, acting as a partial land barrier, is accepted here.

North-East Yorkshire

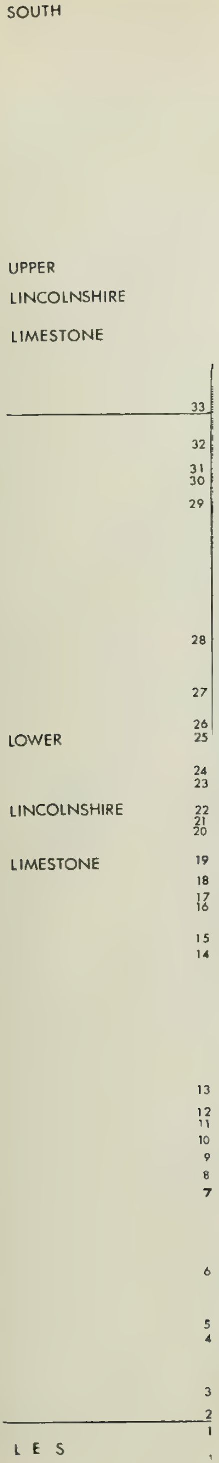
Hydraulic Limestone/Eller Beck Bed

5½ miles north of Market Weighton the Middle Jurassic sediments reappear at Millington and again at Great Givendale, but are only continuous at outcrop from Kirkby Underdale, 3½ miles farther north.

The succession of beds in this part of the Jurassic outcrop is indicated in Table 2. At the base there is a marine sandstone known as the Dogger. This bed does not

STAGE	SOUTH	N.E. INLAND	N.E. COASTAL	N.E CENTRAL
CALLOVIAN	Upper Estuarine Series	Cornbrash?	Cornbrash	Cornbrash
BATHONIAN		Upper Deltaic Series	Upper Deltaic Series	Upper Deltaic Series
BAJOCIAN		Grey Limestone Series	Grey Limestone Series	Grey Limestone Series
		Middle Deltaic Series (Upper)	Middle Deltaic Series (Upper)	Middle Deltaic Series
	Cave Oolite	Upper Limestone	Yons Nab Beds	
		Whitwell Oolite	Millepore Oolite	
	Basement Beds	Middle Deltaic Series (Lower)	Middle Deltaic Series (Lower)	
	Hydraulic Limestone	Eller Beck Bed / Hydraulic Limestone	Eller Beck Bed / Hydraulic Limestone	Eller Beck Bed
	Lower Estuarine Series	Lower Deltaic Series	Lower Deltaic Series	Lower Deltaic Series
		Dogger	Dogger	Dogger
TOARCIAN	Lias	Lias	Lias	Lias

TABLE 2. Succession of Middle Jurassic strata in Yorkshire.


SOUTH
UPPER
LINCOLNSHIRE
LIMESTONE
LOWER
LINCOLNSHIRE
LIMESTONE
L E S

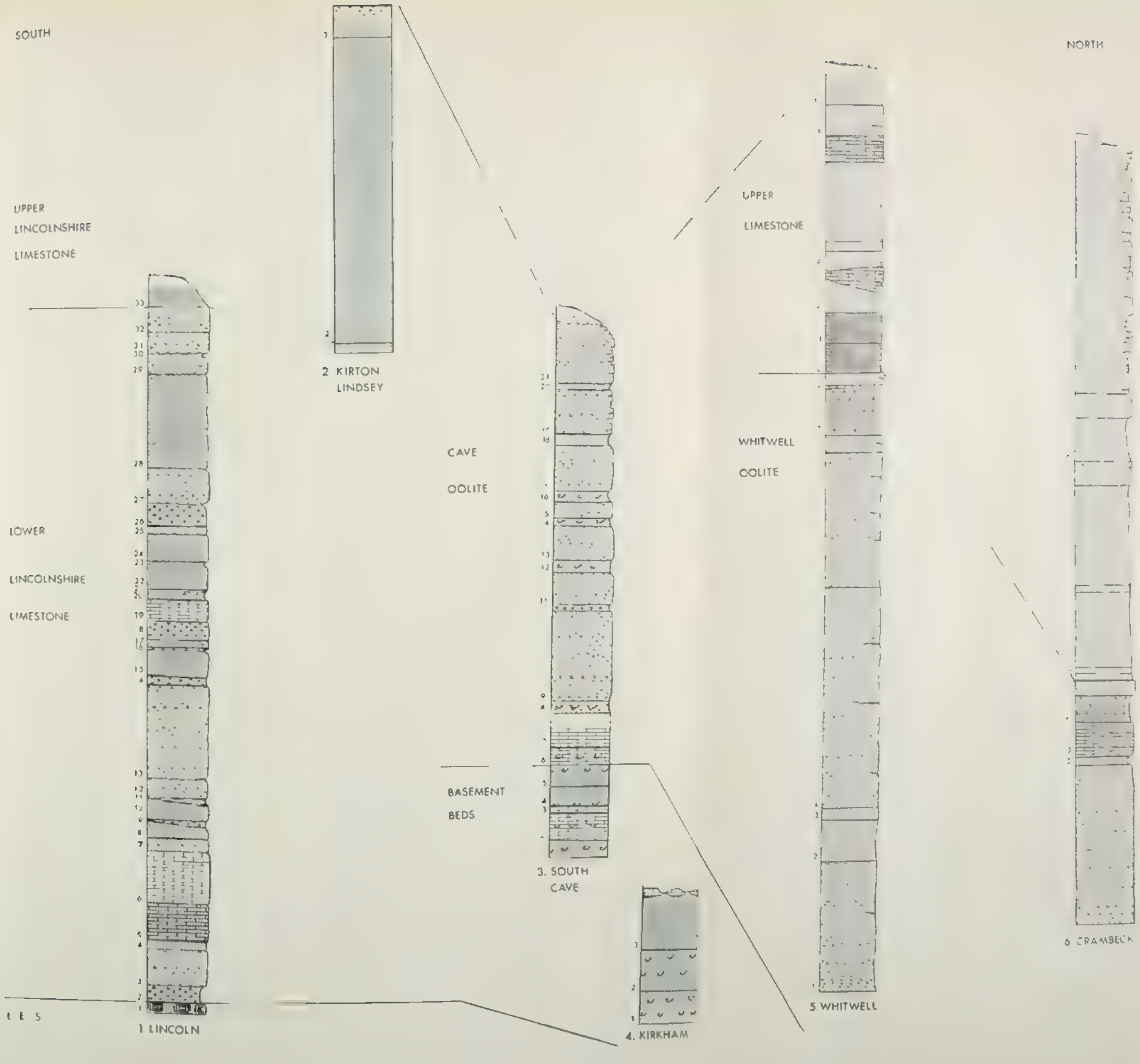

SOUTH
NORTH
UPPER LINCOLNSHIRE LIMESTONE
LOWER LINCOLNSHIRE LIMESTONE
L E S
1 LINCOLN
2 KIRTON LINDSEY
CAVE OOLITE
BASEMENT BEDS
3. SOUTH CAVE
4. KIRKHAM
UPPER LIMESTONE
WHITWELL OOLITE
5 WHITWELL
6 CRAMBECK

Fig. 2 Sections 1–6.

appear to be developed south of Acklam, but as it is of no particular importance here will not be dealt with further.

Overlying the Dogger is the first evidence of the northern delta, the Lower Deltaic Series. This deltaic sequence is the first of three major deltaic episodes which interfinger with marine incursions entering from the east and south-east. The source of the deltaic sediments lies to the north of the Yorkshire Basin. The Lower Deltaic Series varies in thickness from about 50 ft. at Acklam in the south-west to as much as 160 ft. in the north.

Above the Lower Deltaic Series comes the first marine episode, represented by the Hydraulic Limestone, in lithology exactly the same as in the South Cave area. Outcrops are rare and for the most part the course of the limestone is traced only on a break in land slope and by fragments which commonly occur at the surface. The only outcrop encountered here was at Kirkham (section No. 4), although loose debris from an early working on the hillside behind Castle Howard Station, map reference SE/737668, provided a good source.

The Hydraulic Limestone is found at the surface only along the western flanks of the Yorkshire Basin (the centre being obscured by Alluvium of the Vale of Pickering). In the east it probably occurs out to sea but has been found in the Fordon borehole (Falcon & Kent 1960 : 27, where it was incorrectly named the Ellerbeck Bed) as a 4 ft. bed of cementstone. In the west the Hydraulic Limestone facies is recognizable as far north as Skipton Hill on the western flanks of the Hambleton Hills. To the north of this region a marine horizon is recognizable, represented by a thick, ripple-marked sandstone with associated fossiliferous ironstone bands, known under the single name of Eller Beck Bed, after the type locality on the Eller Beck (section No. 11). This facies is found over the whole of the north-central outcrop of the Middle Jurassic and in the coastal exposures to the east, where a good section was measured close to Hayburn Wyke (section No. 9). The Eller Beck Bed facies outcrops to the south of Hayburn but does not extend as far south as Cloughton, the outcrop striking out to sea. The Hydraulic Limestone facies correlated with the Eller Beck Bed by Fox-Strangways (1892 : 194, pl. 4) almost certainly comes in again (out to sea) a few miles south of Cloughton.

The Millepore/Whitwell Oolite

One of the more important marine horizons in the Yorkshire Basin is that represented by oolitic sediments known locally in the east as the Millepore Oolite and in the west as the Whitwell Oolite. Although geographically isolated these beds have long been correlated (Wright 1860 : 32 ; Fox-Strangways 1892 : 206). The Millepore/Whitwell Oolite horizon is separated from the Hydraulic Limestone/Eller Beck Bed horizon below by deltaic sediments of the Lower Middle Deltaic Series and overlain by sediments of the Upper Middle Deltaic Series. As the oolitic horizon does not, in fact, extend all over the northern part of the Basin, in that part the Upper and Lower Middle Deltaic Series are not identifiable as separate units.

In the east the Millepore Oolite first appears at outcrop in Gristhorpe Bay with the best section exposed at Yons Nab headland (section No. 7). The Millepore Oolite is, however, present at depth in the Fordon borehole (Falcon & Kent 1960), where

57 ft. of oolite and sandstone is recorded. At Yons Nab the Millepore Oolite is represented by 15 ft. of false-bedded oolite and overlain by 25 ft. of marine sandstone and shale known as the Yons Nab Beds, a name first introduced by Sylvester-Bradley (1953 : 37). These contain a rich shallow water lamellibranch fauna as well as plentiful ostracods and plant remains. The Millepore Oolite is well developed at Osgodby Nab, the northern headland of Cayton Bay, but is there overlain by 20–30 ft. of deltaic sandstone and not by the Yons Nab Beds. This sandstone probably represents a contemporaneous deltaic distributary (Bate 1959 : 163). At Cloughton Wyke, seven miles to the north, a reduced thickness of the Millepore Oolite (10 ft. 1 in.) is overlain by 7 ft. 6 ins. of arenaceous shale and sandstone containing marine fossils. This upper marine horizon, equivalent to the Yons Nab Beds, can be seen to pass laterally into a typical deltaic sandstone only a few hundred yards from the section. The Millepore Oolite similarly passes laterally northwards into a pure sandstone facies which at Ravenscar (section No. 10) still contains casts of marine fossils, e.g. " *Trigonia* " sp. Farther north it is impossible to distinguish this horizon from the deltaic sandstones of the region.

Along the western outcrop of the Middle Jurassic the oolitic facies is known as the Whitwell Oolite after its development at Whitwell (section No. 5). The rock is a coarse-grained oolite here often massively bedded and developing some clay beds towards the top. Some 33 ft. 9 ins. of sediment belonging to the Whitwell Oolite can be seen, together with 11 ft. 9 ins. of sand and sandy oolite which occur above. At Crambeck (section No. 6), ½ mile to the east, only the upper part of the Whitwell Oolite is exposed together with a more complete development of the overlying beds which consist of 12 ft. of sand and sandstone, a 1 ft. limestone bed and 11–12 ft. of flaggy oolite, the latter termed the Upper Limestone by Hudleston (1873 : 327) and retained here to incorporate the limestone and the underlying sands. The Upper Limestone is a localized upper division of the Whitwell Oolite comparable to the Yons Nab Beds in the east, and may be traced northwards for a distance of about 10 miles and southwards for about 2 miles from the Whitwell Quarries. From Burythorpe the Whitwell Oolite may be traced to Kirkby Underdale as a continuous outcrop and as an isolated outlier at Great Givendale. Although the Millepore Oolite in the east thickens to the south (see Fordon borehole) the Whitwell Oolite appears to thin onto the Market Weighton structure.

Like the Millepore Oolite the Whitwell Oolite, when traced northwards, becomes progressively more sandy until at Kirkby Knowle it is nothing more than a false-bedded coarse-grained sandstone identified more on its position in relation to other beds than on its fossil content.

The stratigraphy and palaeogeography of the other important marine horizon of the Yorkshire Middle Jurassic, the Grey Limestone Series, have been dealt with elsewhere (Bate 1965).

III STRATIGRAPHICAL SECTIONS

All the ostracods listed below have been described by Bate (1963, 1963*a*, 1964) and are represented in the collections of the Department of Palaeontology, British Museum (Natural History).

SECTION NO. 1. Lower Lincolnshire Limestone (Text-fig. 2), complete section in Greetwell Quarry, Lincoln, of the Blue and Silver Beds and of the Kirton Cementstone Series.

Kirton Cementstone Series

	ft.	in.
33. Soft grey marl passing upwards into subsoil. Ostracods abundant: *Bairdia hilda, Progonocythere cristata, Ektyphocythere triangula, Cytherella fullonica* and *Praeschuleridea subtrigona subtrigona* seen to	1	0
32. Massive grey oolitic limestone	1	3
31. Coarse white oolite with abundant shells	1	2
30. Yellow marl with ooliths. Ostracods: *Aulacocythere punctata, Cytheromorpha ? greetwellensis, Progonocythere cristata, Systenocythere exilofasciata, Dolocythere maculosa, Praeschuleridea subtrigona subtrigona, Fuhrbergiella* (*Praefuhrbergiella*) *arens* and *Ektyphocythere triangula*	0	1
29. Coarse white oolite. Ostracods: *Aulacocythere punctata, Systenocythere exilofasciata, Pneumatocythere carinata, Dolocythere maculosa, Bairdia hilda* and *Praeschuleridea subtrigona subtrigona*	1	0
28. Coarse rubbly oolite. Ostracods: *Fuhrbergiella* (*P.*) *arens, Systenocythere exilofasciata, Pneumatocythere carinata, Micropneumatocythere convexa, Southcavea reticulata, Asciocythere lacunosa, Dolocythere maculosa* and *Praeschuleridea subtrigona subtrigona*	4	6
27. Shelly blue-hearted oolite. Corals and horizontal burrows	1	9
26. Grey oolitic shale with wedges of marl. Ostracods: *Dolocythere maculosa, Pneumatocythere bajociana, Acanthocythere* (*Protoacanthocythere*) *faveolata, Micropneumatocythere convexa, Systenocythere exilofasciata, Aulacocythere punctata* and *Praeschuleridea subtrigona subtrigona*	1	3–10
25. Coarse shelly oolite with fragments of marlstone. Ostracods: *Ektyphocythere triangula, Asciocythere lacunosa, Monoceratina vulsa, Eocytheridea faveolata, E. reticulata* & *E. lacunosa, Micropneumatocythere globosa* & *M. convexa, Aulacocythere punctata, Dolocythere maculosa, Systenocythere exilofasciata, Pneumatocythere bajociana, Camptocythere lincolnensis, Cytheropterina comica* & *C. gravis, Praeschuleridea subtrigona subtrigona* and *P. ventriosa*	0	8
24. White marlstone. Ostracods rare: *Pneumatocythere bajociana* and *Praeschuleridea subtrigona subtrigona*	1	8
23. Chocolate-brown marl, weathering grey. Ostracods rare: *Pneumatocythere bajociana* and *Micropneumatocythere globosa*	0	2
22. White marlstone. Ostracods rare: *Praeschuleridea subtrigona subtrigona* + indet. species	1	2

	ft.	*in.*
21. Chocolate-brown, weathering grey marl. Ostracods rare: *Pneumatocythere bajociana* and *Dolocythere maculosa*	0	2
20. Rubbly white marl with scattered ooliths. Ostracods common: *Praeschuleridea subtrigona subtrigona, Pneumatocythere bajociana, Micropneumatocythere globosa, Dolocythere maculosa, Systenocythere exilofasciata, Cytheropterina comica, Ektyphocythere triangula, Cytherelloidea catenulata, Paracypris bajociana, Monoceratina vulsa* and *Acanthocythere* (*P.*) *faveolata*	0	5
19. Blue-hearted fine-grained limestone weathering cream. *Nerinea* and lamellibranch shells common. Scattered ooliths. Ostracods rare: *Micropneumatocythere convexa* and *Cytherelloidea catenulata*	1	2
18. Grey marl with scattered ooliths and marlstone fragments. Ostracods: *Dolocythere maculosa, Pneumatocythere bajociana, Ektyphocythere triangula* and *Praeschuleridea subtrigona subtrigona*.	0	9
17. White marlstone with abundant ostracods: *Praeschuleridea subtrigona subtrigona* & *P. ventriosa, Ektyphocythere triangula, Cytheropterina comica* & *C. gravis, Pneumatocythere bajociana, Acanthocythere* (*P.*) *faveolata, Systenocythere exilofasciata, Dolocythere maculosa, Micropneumatocythere globosa* and *Cytherelloidea eastfieldensis*	0	8
16. Oolitic marl. Ostracods: *Pneumatocythere bajociana, Praeschuleridea subtrigona subtrigona, Dolocythere maculosa, Systenocythere exilofasciata, Cytheropterina comica* and *Micropneumatocythere globosa*	0	1
15. White marlstone with scattered ooliths. Ostracods: *Platella jurassica, Cytheropterina gravis, Acanthocythere* (*P.*) *faveolata, Eocytheridea faveolata, Micropneumatocythere globosa, Ektyphocythere triangula, Cytherelloidea catenulata, Systenocythere exilofasciata* and *Praeschuleridea subtrigona subtrigona*	1	7
14. Shaly oolitic marl. Ostracods: *Systenocythere exilofasciata, Pneumatocythere bajociana, Camptocythere lincolnensis, Cytheropterina gravis, Micropneumatocythere globosa* and *Dolocythere maculosa*	0	3
Blue and Silver Beds		
13. Cream limestone with scattered ooliths, passing laterally into more coarsely oolitic limestone. In part also a shelly limestone. Ostracods not common: *Micropneumatocythere globosa, Cytherelloidea catenulata* and *Praeschuleridea subtrigona subtrigona*.	4	9
12. Fine grained limestone with scattered ooliths	0	11
11. Sandy shale—no microfauna	0	0–2

	ft.	*in.*
10. Cream marlstone with shells and scattered ooliths. Ostracods: *Cytheropterina comica* & *C. gravis*, *Systenocythere exilofasciata*, *Praeschuleridea subtrigona subtrigona*, *Cytherella fullonica*, *Camptocythere lincolnensis*, *Pneumatocythere bajociana*, *Fuhrbergiella* (*P.*) *arens* and *Bairdia hilda*	0	9
9. Brown clay with ooliths. Ostracods rare: *Systenocythere exilofasciata*, *Camptocythere lincolnensis*, *Pneumatocythere bajociana*, *Fuhrbergiella* (*P.*) *arens*, *Cytherella fullonica*, *Cytherelloidea catenulata*, *Cytheropterina comica*, *Ektyphocythere triangula* and *Dolocythere maculosa*	0	1–4
8. Cream marly bed with scattered ooliths. Ostracods: *Praeschuleridea subtrigona subtrigona*, *Dolocythere maculosa* and *Systenocythere exilofasciata*	0	6
7. Coarse, cream oolite with reddish colour banding and vertical pipes. Ostracods: *Cytheropterina gravis* and *Praeschuleridea subtrigona subtrigona*	0	6
6. Blue hearted fine grained limestone with cream weathering surface. Ooliths and shell fragments present throughout. Ostracods: *Systenocythere exilofasciata*, *Cytheropterina gravis* and indet. species	2	6
5. Sandy limestone with coarse ooliths	1	8
4. Fine grained, ochre coloured sandstone	0	5
3. Ferruginous oolite	1	8
Lower Estuarine Series		
2. Grey-green oolitic clay	0	10
Northampton Sand Ironstone		
1. Oolitic ironstone with Boxstones and concretions. seen to	0	6

Section No. 2. Complete section through the Kirton Shale, Kirton Cement Quarry, Kirton Lindsey (Text-fig. 2).

3. Base of Hibaldstow Oolite.		
2. Kirton Shale. Black clay, becoming brownish-buff in upper 3 feet. Ostracods extremely abundant: *Acanthocythere* (*P.*) *faveolata*, *Aulacocythere punctata* & *A. reticulata*, *Dolocythere maculosa*, *Bairdia hilda*, *Monoceratina vulsa* & *M.* cf. *scrobiculata*, *Ektyphocythere triangula*, *Praeschuleridea subtrigona subtrigona*, *Paracypris bajociana*, *Progonocythere cristata*, *Kirtonella plicata*, *Cytherella fullonica*, *Cytheromorpha* ? *greetwellensis*, *Cytherelloidea catenulata*, *Platella jurassica*, *Pleurocythere kirtonensis* & *P. nodosa* and *Fuhrbergiella* (*P.*) *arens*	14	0
1. Top of Kirton Cementstone Series.		

Section No. 3. Cave Oolite, Eastfield Quarry, South Cave, Yorkshire. Almost complete section through the Cave Oolite and (in 1947) partial section through the underlying marls (Text-fig. 2).

Cave Oolite

		ft.	*in.*
21.	Flaggy oolite, rather coarse grained and compact. Shell fragments, no ostracods . . . . seen to	3	0
20.	Sandy marl	0	3
19.	Cream, sandy, oolitic limestone, flaggy with shells and plant remains. Ostracods present but poorly preserved and indeterminate	2	3
18.	Yellow-brown sandy marl with cream oolitic marlstone band. Ostracods present in both lithologies : *Ektyphocythere triangula*, *Aulacocythere punctata*, *Micropneumatocythere globosa*, *Systenocythere exilofasciata*, *Fuhrbergiella* (*P.*) *arens*, *Eocytheridea elongata*, *Praeschuleridea subtrigona subtrigona*, *Southcavea reticulata* and *S. bajociana*	0	7
17.	Fine grained creamy limestone, oolitic	2	3
16.	Shell sand with purple marly parting at top. Ostracods : *Micropneumatocythere convexa*, *M. globosa*, *Aulacocythere punctata*, *Praeschuleridea subtrigona subtrigona*, *Systenocythere exilofasciata*, *Southcavea reticulata* and *S. grandis*	0	3–5
15.	Shelly oolite. Ostracods : *Eocytheridea* ? *astricta*, *Praeschuleridea subtrigona subtrigona*, *Dolocythere maculosa*, *Fuhrbergiella* (*P.*) *arens*, *Pleurocythere nodosa*, *Micropneumatocythere convexa*, *Aulacocythere punctata*, *Southcavea bajociana*, *S. reticulata*, *Asciocythere lacunosa* and *A. acuminata*	0	11
14.	Shell sand with purple marly partings at top. Ostracods : *Aulacocythere punctata*, *Southcavea reticulata*, *Micropneumatocythere convexa*, *Praeschuleridea subtrigona subtrigona*, *Pneumatocythere carinata*, *Ektyphocythere triangula*, *Fuhrbergiella* (*P.*) *arens* and *Dolocythere maculosa*	0	7
13.	Blue hearted creamy limestone. Shelly and in part oolitic . .	1	9
12.	Ochre coloured shell sand with *Pentacrinus* ossicles, echinoid spines and shell fragments. Ostracods : *Pneumatocythere carinata*, ?*Pneumatocythere bajociana*, *Praeschuleridea subtrigona magna*, *Aulacocythere punctata*, *Fuhrbergiella* (*P.*) *arens*, *Southcavea reticulata*, *S. grandis*, *Eocytheridea carinata*, *E. elongata*, *Asciocythere lacunosa*, *Dolocythere maculosa*, *Systenocythere exilofasciata*, *Ektyphocythere triangula* and *Acanthocythere* (*P.*) *faveolata*	0	8
11.	Blue hearted, coarsely oolitic limestone. Ostracods : *Dolocythere maculosa* and *Praeschuleridea subtrigona magna* . . .	1	8

	ft.	in.
10. Creamy-yellow, oolitic limestone, very fossiliferous and crowded with *Pentacrinus* ossicles. Ostracods: *Asciocythere lacunosa, Praeschuleridea subtrigona magna, Southcavea bajociana, S. grandis, S. reticulata, Cytherelloidea catenulata, Pleurocythere nodosa, Ektyphocythere triangula, Paracypris bajociana, Systenocythere exilofasciata, Bairdia hilda, Micropneumatocythere convexa, Dolocythere maculosa, Fuhrbergiella* (*P.*) *arens, Eocytheridea* ? *astricta, E. elongata* and *E. carinata*	0	3
9. Coarsely oolitic cream oolite. Ostracods: *Monoceratina vulsa, Praeschuleridea subtrigona subtrigona, Paracypris bajociana* and indeterminate ostracods	4	8
8. Shelly, coarsely oolitic limestone. Ostracods: *Southcavea bajociana* & *S. reticulata, Eocytheridea carinata* & *E. faveolata, Aulacocythere punctata, Micropneumatocythere globosa, M. convexa, Paracypris bajociana, Ektyphocythere triangula, Fuhrbergiella* (*P.*) *arens, Asciocythere acuminata, Praeschuleridea subtrigona subtrigona, Systenocythere exilofasciata, Dolocythere maculosa, Acanthocythere* (*P.*) *faveolata* and *Pneumatocythere carinata*	0	9

Base of Cave Oolite section as seen in Eastfield Quarry. Section continued in sump excavated in 1947. Details of section from Professor P. C. Sylvester-Bradley.

Basement Beds

	ft.	in.
7. Rubbly pellety limestone with lamellibranchs . . seen to	0	10
6. Ferruginous limestone full of shells	0	11
5. Ferruginous marl full of lamellibranchs and crinoid stems. This marl has been dumped by the side of the sump and has provided the following ostracod fauna: *Cytherelloidea eastfieldensis, Paracypris bajociana, Progonocythere reticulata, Monoceratina vulsa, Acanthocythere* (*P.*) *faveolata, Aulacocythere punctata, Micropneumatocythere convexa, Pneumatocythere bajociana, Pleurocythere kirtonensis, Pleurocythere* sp., *Dolocythere maculosa, Homocytheridea cylindrica, Tetracytheridea punctata, Asciocythere lacunosa, Eocytheridea elongata, E. lacunosa, E.* ? *astricta, E.* ? *erugata, Paraschuleridea ornata, Paraschuleridea* sp., *Praeschuleridea ventriosa, Cytheropterina comica, C. gravis, Ektyphocythere triangula, Southcavea bajociana* and *Systenocythere exilofasciata* .	1	2
4. Shale, shelly at base, marlstone impersistant at top . . .	1	2
3. Nodular limestone with lamellibranchs	0	2–3
2. Grey limestone full of gastropods and crushed lamellibranchs .	1	4
1. Shelly shale. Ostracods: *Progonocythere reticulata, Eocytheridea lacunosa, Praeschuleridea ventriosa, Asciocythere lacunosa, A. acuminata, Cytheropterina comica, Micropneumatocythere convexa,*		

	ft.	*in.*
Pneumatocythere bajociana, *Dolocythere maculosa* and *Ektyphocythere triangula* . . . . seen to	1	0

SECTION NO. 4. Hydraulic Limestone and associated marls exposed in a road cutting at Kirkham. The Firby Road section (Text-fig. 2). These sediments come below the marine succession exposed in the Eastfield Quarry, South Cave, and occur to the north of the Market Weighton structure.

4. Hydraulic Limestone—occurring below the level of the subsoil as isolated boulders of greyish-white porcellaneous limestone. Ostracods : *Ektyphocythere triangula*, *Praeschuleridea subtrigona subtrigona*, *Cytheropterina comica*, *Micropneumatocythere globosa*, *Kirtonella plicata* and *Progonocythere cristata*.		
3. Grey clay. Ostracods : *Kirtonella plicata*, *Asciocythere lacunosa*, *Tetracytheridea punctata* and *Eocytheridea lacunosa*	4	0
2. Ironstone-mudstone. Lamellibranchs present throughout. Ostracods : *Progonocythere* cf. *reticulata*, *Cytheropterina gravis*, *Praeschuleridea subtrigona subtrigona*, *P. ventriosa*, *Asciocythere lacunosa* and *Micropneumatocythere globosa*	2	0
1. Grey calcareous sandstone with shells. Ostracods : *Progonocythere reticulata*, *Cytheropterina gravis*, *Praeschuleridea subtrigona subtrigona*, *P. ventriosa*, *Asciocythere lacunosa*, *Eocytheridea lacunosa*, *E.* ? *erugata*, *Paracypris bajociana* and *Pneumatocythere bajociana* . . . . seen to	2	0

SECTION NO. 5. Whitwell Oolite, Seamer Lime and Stone Co. Quarry, Whitwell. Almost complete section through the Whitwell Oolite and the base of the Upper Limestone (Text-fig. 2).

Upper Limestone

19. Yellow sand	1	4
18. Yellow, flaggy sandstone with interbedded sand.	1	7
17. Sandy limestone—almost a calcareous sandstone. Ostracod : *Praeschuleridea subtrigona magna*	1	3
16. Yellow, false-bedded sand with thin lamellae of clay at base . .	4	0
15. Clay	0	5
14. False-bedded, yellow sand	0	10
13. Lens of flaggy sandy limestone. Ostracods : *Southcavea reticulata*, *Progonocythere cristata* and *Praeschuleridea subtrigona magna* .	1	4
12. False-bedded sand	1	0
11. Alternating bands of white sand and chocolate-brown clay . .	1	5
10. Alternating bands of yellow sand and brown clay	1	5

SOUTH

YONS NAB BEDS

MILLEPORE OOLITE

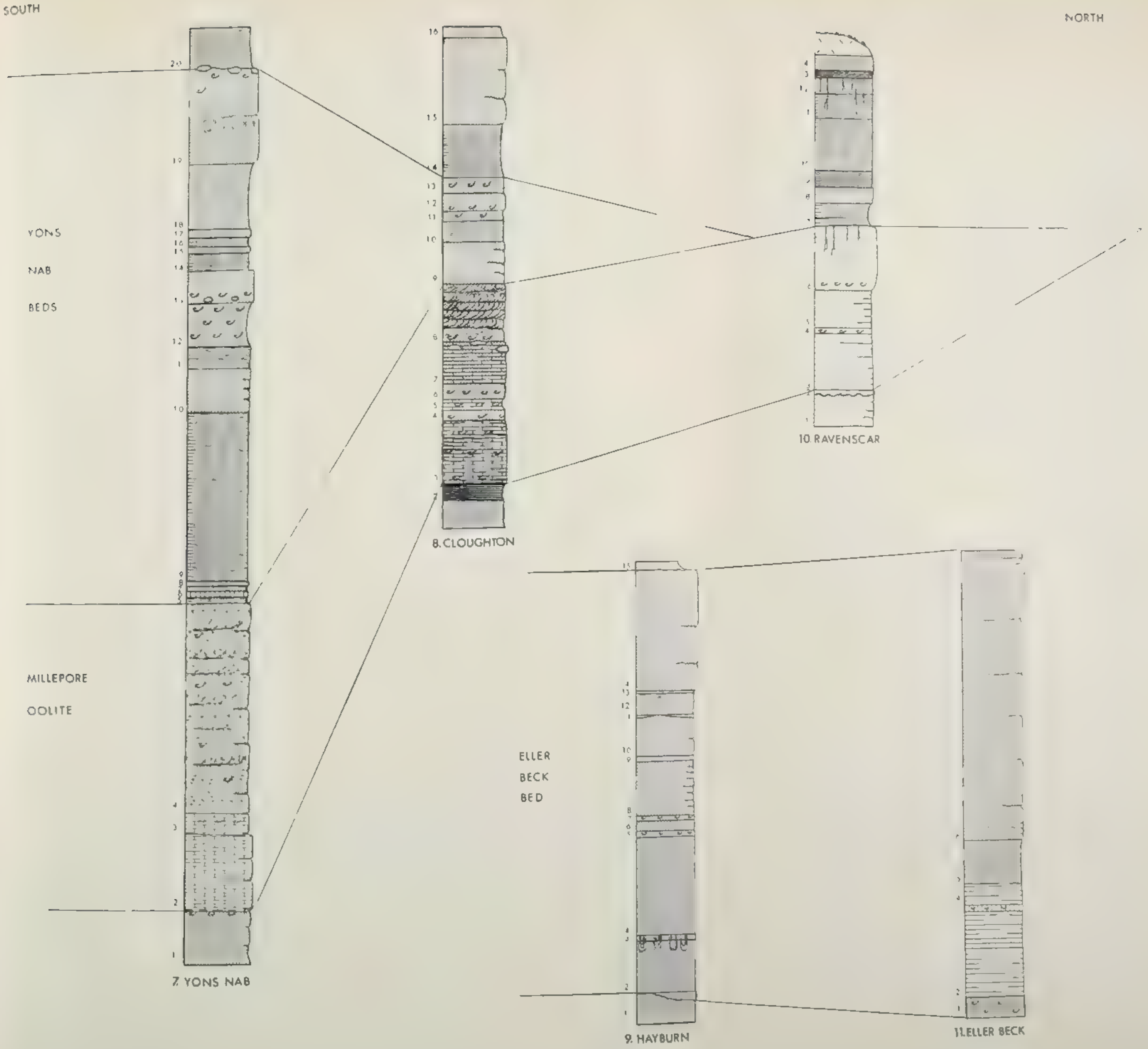

SOUTH
NORTH
YONS
NAB
BEDS
MILLEPORE
OOLITE
ELLER
BECK
BED
7. YONS NAB
8. CLOUGHTON
10. RAVENSCAR
9. HAYBURN
11. ELLER BECK

FIG. 3. Sections 7–11.

Whitwell Oolite

	ft.	in.
9. Flaggy, sandy oolite. Ostracods : *Progonocythere cristata, Praeschuleridea subtrigona magna, Eocytheridea lacunosa* and *Micropneumatocythere globosa*	0	8
8. Purple oolitic clay	0	2
7. Grey oolitic clay. Ostracods : *Praeschuleridea subtrigona magna, Eocytheridea elongata, E. ? erugata, E. ? astricta, Micropneumatocythere globosa* and *Pneumatocythere bajociana* . . .	2	5
6. Flaggy oolite, ironstained in parts. Surface showing ripple markings. Ostracods : *Eocytheridea faveolata* and *Praeschuleridea subtrigona magna*	0	10
5. White-weathering, soft, coarsely oolitic limestone. Ostracods : *Praeschuleridea subtrigona magna, Dolocythere maculosa, Systenocythere exilofasciata, Kirtonella reticulata, Eocytheridea ? erugata, E. faveolata, E. carinata, Fuhrbergiella (P.) minima, Micropneumatocythere globosa, Monoceratina vulsa* and *Pleurocythere kirtonensis*	6	9
4. Cream weathering, blue hearted oolite. Ostracods : *Kirtonella reticulata, Praeschuleridea subtrigona magna, Eocytheridea ? erugata, E. ? astricta, E. carinata, Micropneumatocythere convexa, M. globosa, Systenocythere exilofasciata, Monoceratina vulsa, Fuhrbergiella (P.) minima, Paracypris bajociana, Aulacocythere punctata, Cytherelloidea catenulata, Ektyphocythere triangula* and *Dolocythere maculosa*	11	0
3. Yellow-brown sandstone. Ostracods : *Praeschuleridea subtrigona magna* and *Micropneumatocythere globosa*	0	7
2. Yellow sand with shells at top	2	0
1. False-bedded, coarsely oolitic limestone. Ostracods : *Progonocythere cristata, Praeschuleridea subtrigona magna, Eocytheridea ? astricta, E. carinata, Fuhrbergiella (P.) minima, Micropneumatocythere globosa* and *Paracypris bajociana* . . seen to	6	6

Section No. 6. Upper Limestone and Whitwell Oolite exposed at Crambeck. The section through the Upper Limestone is almost complete (Text-fig. 2.).

Upper Limestone

10. Thin, flaggy, oolitic limestone. Ostracods : *Eocytheridea ? erugata, Micropneumatocythere globosa, Praeschuleridea subtrigona magna, Cytheropterina plana* and incertae sedis . . . .about	10–12	0
9. Yellow sandstone	1	2
8. Soft yellow sand	2	0

	ft.	in.
7. Flaggy sandy oolite. Ostracods: *Eocytheridea* ? *acuta*, *Micropneumatocythere globosa*, *Dolocythere maculosa*, *Praeschuleridea subtrigona magna*, *Kirtonella reticulata* and *Pneumatocythere carinata*	1	0
6. Yellow sandstone and unconsolidated sand	9	0

Whitwell Oolite

	ft.	in.
5. Hard, crystalline limestone	0	7
4. Sandy oolite. Ostracods: *Micropneumatocythere globosa*, *Praeschuleridea subtrigona magna* and *Systenocythere exilofasciata*	1	3
3. Sandy limestone	1	9
2. Soft yellow sand	0	5
1. Coarse creamy oolite. Ostracods: *Eocytheridea carinata*, *E.* ? *erugata*, *Micropneumatocythere globosa*, *Praeschuleridea subtrigona magna*, *Dolocythere maculosa*, *Pneumatocythere carinata* and *Paracypris bajociana* seen to	6	7

Section No. 7. Complete section through the Millepore Oolite and the overlying Yons Nab Beds exposed along the foreshore at Yons Nab headland (Text-fig. 3). For the list of macrofossils obtained from this section see Bate (1959 : 158–9).

	ft.	in.
20. Grey shale of the Upper Middle Deltaic Series	2	4

Yons Nab Beds

	ft.	in.
19. Medium-grained grey sandstone, ironstained in the upper 12 inches with ironstone nodules and fossil casts; worm burrows in the lower 3½ feet	4	5
18. Grey sandy shale	3	0
17. Ironstone band	0	3
16. Grey sandy shale	0	5
15. Ironstone band	0	2
14. Sandy shale	0	9
13. Argillaceous sandstone with ironstone nodules at the base. Southwards this bed grades laterally into a sandy limestone. Ostracods: *Progonocythere cristata*, *Pneumatocythere bajociana*, *Eocytheridea lacunosa*, *E. faveolata*, *E.* ? *astricta*, *E.* ? *acuta*, *Micropneumatocythere convexa*, *Systenocythere exilofasciata*, *Dolocythere maculosa* and *Praeschuleridea subtrigona magna*	1	6
12. Highly fossiliferous grey shale with white shells. Ostracods: *Progonocythere cristata*, *Pneumatocythere bajociana*, *Paracypris bajociana*, *Micropneumatocythere globosa*, *Kirtonella plicata* and *Praeschuleridea subtrigona magna*	2	0
11. Sandy, micaceous, grey shale	1	0

	ft.	in.
10. Yellow micaceous sandstone with plant remains and ripple markings	2	1
9. Grey, sandy shale with plant remains	8	0
8. Ironstone band	0	2
7. Grey shale	0	5
6. Mudstone band	0	3
5. Grey shale. Ostracods common : *Cytheropterina plana, Pneumatocythere bajociana, Micropneumatocythere globosa, Paracypris bajociana, Systenocythere exilofasciata, Ektyphocythere triangula, Asciocythere lacunosa, Kirtonella reticulata, Eocytheridea lacunosa. E. ? erugata, E. ? astricta, E. carinata, Dolocythere maculosa, Homocytheridea cylindrica, Praeschuleridea ventriosa* and *P. subtrigona magna*.	0	4

Millepore Oolite

4. Coarse, false-bedded, shelly oolite. Ostracods : *Progonocythere cristata, Pneumatocythere carinata & P. bajociana, Micropneumatocythere globosa, Monoceratina* cf. *vulsa, Eocytheridea faveolata, E. ? erugata, E. lacunosa, E. ? astricta, Dolocythere maculosa* and *Praeschuleridea subtrigona magna*	10	0
3. Grey, shelly oolite. Ostracods : *Micropneumatocythere globosa, Paracypris bajociana, Eocytheridea carinata* and *Praeschuleridea subtrigona magna*.	1	0
2. Fine-grained limestone. Ostracods : *Systenocythere exilofasciata, Eocytheridea lacunosa* and *Praeschuleridea subtrigona magna*	3	6

Lower Middle Deltaic Series

1. Yellow sandstone, the top 6 inches containing crinoid ossicles seen to	2	0

Section No. 8. Complete section through the Millepore Oolite and the overlying Yons Nab Beds. Section exposed at Cloughton Wyke, along the foreshore and at the base of the low cliff (Text-fig. 3).

Upper Middle Deltaic Series

16. Sandy shale seen to	1	0
15. Yellow, false-bedded sandstone with plant roots	4	2

Yons Nab Beds

14. Sandy shale, indet. ostracods	2	5
13. Grey-black, ironstained, fossiliferous shale with coal. Lamellibranch casts abundant. Ostracods mainly represented by internal costs : *Praeschuleridea subtrigona magna*	0	9

		ft.	in.
12.	Thinly-bedded sandstone with fossil casts and indeterminate ostracods	0	10
11.	Grey-black, ironstained shale, very fossiliferous. Lamellibranch and ostracod casts	0	5
10.	Sandy shale with thin sandstone bands. Fossil casts and plant remains. Ostracods indeterminate	1	0
9.	Flaggy sandstone with plant remains	2	1

Millepore Oolite

		ft.	in.
8.	Yellow, false-bedded sandstone with fossil casts at the base	2	8
7.	Sandy limestone with ironstone nodules in the upper part. Ostracods : *Eocytheridea lacunosa, E.* ? *erugata, E.* ? *acuta, E.* ? *astricta, E. carinata, Micropneumatocythere globosa, Praeschuleridea subtrigona magna, Dolocythere maculosa, Cytheropterina plana, Kirtonella reticulata, Southcavea reticulata, Ektyphocythere triangula* and *Paracypris bajociana*	1	10
6.	Fossiliferous mudstone. Ostracods : *Eocytheridea carinata, E.* ? *astricta, Micropneumatocythere convexa, M. globosa, Praeschuleridea subtrigona magna, Fuhrbergiella* (*P.*) *minima* and *Kirtonella reticulata*	0	9
5.	Fossiliferous limestone. Ostracods : *Eocytheridea* ? *erugata, E. carinata, E.* ? *astricta, Micropneumatocythere globosa, Praeschuleridea subtrigona magna, Dolocythere maculosa, Fuhrbergiella* (*P.*) *minima, Cytheropterina plana, Kirtonella reticulata* and ?*Homocytheridea cylindrica*	0	6
4.	Yellow sandstone with fossil casts	0	7
3.	Fine-grained, fossiliferous, calcareous mudstone. Ostracods : *Micropneumatocythere globosa, Eocytheridea* ? *astricta, Praeschuleridea subtrigona magna* and ?*Monoceratina vulsa*	3	0
2.	Dark-grey shale. Ostracods as internal casts	0	9

Lower Middle Deltaic Series

1. Light grey shale.

Section No. 9. Hayburn, complete section through the Eller Beck Bed (Text-fig. 3).

15. Grey shale of the Lower Middle Deltaic Series.

Eller Beck Bed

		ft.	in.
14.	Massive sandstone with ripple markings along bedding planes	5	9
13.	Ironstone band	0	2
12.	Alternating bands of shale and sandstone	0	11
11.	Ironstone band	0	2

	ft.	in.
10. Sandstone	1	10
9. Ironstone band	0	3
8. Flaggy, micaceous sandstone	2	10
7. Fossiliferous ironstone band	0	3
6. Sandstone	0	2
5. Fossiliferous ironstone band	0	3
4. Dark grey shale	4	8
3. Ironstone band from which worm burrows of the same composition pass down into the bed below	0	3
2. Grey shale, with impersistent ironstone at the base	1	0–7

Lower Deltaic Series

1. Grey shale seen to	1	0

Section No. 10. Complete section through the Millepore Bed as exposed at the top of the high cliff at Ravenscar (Text-fig. 3).

Upper Middle Deltaic Series

14. Grey-black shale seen to	0	11
13. Coaly shale	0	5
12. Grey shale with plant roots extending from bed 13	0	8
11. Sandy shale with plant roots	0	9
10. Sandy shale	2	5
9. Ironstained shale	0	9
8. Yellow sandstone with plant debris	0	9
7. Grey-black sandy shale, carbonaceous at base	1	2

Millepore Bed

6. Massive sandstone with upper 2 ft. 6 ins. silver ganister containing vertical plant roots. Lower 11 ins. with lamellibranch casts	3	5
5. Flaggy, false-bedded sandstone	1	10
4. Yellow sandstone with fossil casts	0	4
3. Flaggy, yellow, micaceous sandstone	2	8

Lower Middle Deltaic Series

2. Band of doggers, weathering hollow	0	3
1. White, flaggy sandstone seen to	1	6

SECTION No. 11. The type section of the Eller Beck Bed, a complete section exposed in the banks of the Eller Beck (Text-fig. 3).

Eller Beck Bed

		ft.	*in.*
6.	Massive, buff-yellow sandstone with ripple markings along some bedding planes	13–14	0
5.	Sandy shale and thin, flaggy sandstone showing false bedding .	2	2
4.	Dark-grey ironstained shale	1	0
3.	Fossiliferous ironstone band	0	5
2.	Dark-grey ironstained shale	4	2
1.	Fossiliferous ironstone . . . . . . seen to	1	0

IV CORRELATION

The only definite dating of the Oolites at the present time is the recorded occurrence of ammonites of *discites* age in the Lower Lincolnshire Limestone. Arkell (1933 : 214), however, mentions that *Trigonia hemisphaerica* has been found in the Kirton Marl of Kirton Lindsey and that this lamellibranch is to be found in the Cotswolds only in the Lower Trigonia Grit, a bed also of *discites* age. By inference this would suggest that the Lower Lincolnshire Limestone and the base of the Upper Lincolnshire Limestone belong to the single ammonite zone of *Hyperlioceras discites*. Within the Upper Lincolnshire Limestone the only recorded ammonite is stated to be one of the "*humphriesianus-group*" by Cross (1875 : 121) from the Scunthorpe district. No precise locality was given. Kent (personal communication) states that he has been unable to locate this ammonite and the record could be erroneous. The Grey Limestone Series of Yorkshire which is of *humphriesianum* age, certainly in part, has a very different ostracod fauna from that of the Lincolnshire Limestone and hence no part of the latter can be correlated with beds of that age.

Table 4 indicates a general uniformity throughout the Lincolnshire Limestone and the equivalent beds in Yorkshire. It also shows the restriction of *Cytheropterina comica* and *C. gravis* to the Lower Lincolnshire Limestone and the Hydraulic Limestone–Basement Beds horizon in Yorkshire, and the replacement of these species by *C. plana* in the Millepore and Whitwell Oolites. *C. plana* has not yet been found in the Upper Lincolnshire Limestone. *Tetracytheridea punctata* is restricted to the Basement Beds and the horizon below the Hydraulic Limestone but has not yet been recorded from the Lower Lincolnshire Limestone.

Fuhrbergiella (*Praefuhrbergiella*) *minima* is restricted to the Millepore and Whitwell Oolites. *Praeschuleridea subtrigona subtrigona* is now known to be restricted to the Lincolnshire Limestone and a few beds within the Cave Oolite, and is replaced to the north of Market Weighton by the geographic subspecies *P. subtrigona magna*. *Glyptocythere*, abundant within the Grey Limestone Series, is virtually absent from the Lincolnshire Limestone but occurs within the highest beds of the Upper Lincolnshire Limestone. The species there is similar to *G. costata* Bate (1965 : 106) but is much larger. No specific name can yet be given to this ostracod because of indifferent

Stage	North of Market Weighton	South of Market Weighton	North Lincolnshire
BATHONIAN	Upper Deltaic Series	Upper Estuarine Series	Upper Estuarine Series
BAJOCIAN	Grey Limestone Series		Unconformity - beds of equivalent age missing
	Upper Middle Deltaic Series		
	Yons Nab Beds/Upper Limestone Millepore Oolite/Whitwell Oolite	Cave Oolite	Hibaldstow Oolite Kirton Shale (*Acanthothiris crossi* Bed)
	Lower Middle Deltaic Series	Basement Beds	Kirton Cementstone Series Blue & Silver Beds
	Hydraulic Limestone/Eller Beck Bed	Hydraulic Limestone	
	Lower Deltaic Series	Lower Estuarine Series	Lower Estuarine Series
	Dogger	No equivalent, Dogger missing	Northampton Sand

TABLE 3. Correlation of Bajocian sediments of Yorkshire and Lincolnshire. It is possible the highest beds of the Upper Lincolnshire Limestone in South Lincolnshire are of the same age as the Upper Middle Deltaic Series. The Grey Limestone Series is not, however, represented in Lincolnshire.

preservation. From the evidence of the ostracod faunas it is possible to suggest a broad correlation of the Yorkshire and Lincolnshire sediments as indicated in Table 3.

Although the ostracod faunas in the Lower Lincolnshire Limestone, Hydraulic Limestone and associated marls and sandstones, and the Basement Beds are broadly uniform with beds higher in the succession the common occurrence of *C. gravis* and *C. comica* and their restriction to this horizon supports previous stratigraphical correlations. A number of ostracod species peculiar to the Basement Beds are considered to be of local significance only. Correlation of the Hydraulic Limestone with the Eller Beck Bed farther north must be considered solely on stratigraphical grounds as there are no ostracods in the latter marine horizon. This northward facies change from a limestone into a sandstone is to be expected on approaching a delta and will be dealt with in the next section.

The Millepore and Whitwell Oolites have *Fuhrbergiella* (*P.*) *minima* as a common ostracod but otherwise the fauna is basically uniform with that in the Upper and Lower Lincolnshire Limestones. *Cytherelloidea eastfieldensis*, found in the Lower Lincolnshire Limestone and in the Basement Beds is neither represented in the Millepore/Whitwell Oolites nor in the Upper Lincolnshire Limestone. The Yorkshire sediments also appear to have a dominant *Eocytheridea* fauna which may be geographically controlled. One species *E. ?acuta* is entirely restricted to Yorkshire. The Yons Nab Beds and Upper Limestone have the same ostracods as those appearing in the underlying Oolites and must be part of the same marine transgression.

By inference the major part of the Lincolnshire Limestone probably belongs to the

Hyperlioceras discites Zone, although the highest beds of the Upper Lincolnshire Limestone are possibly slightly younger than this. By correlation the two marine horizons in Yorkshire must also be of *discites* age—this is particularly true for the Hydraulic Limestone/Eller Beck Bed horizon, the marine sediments below, the Basement Beds above and the Lower Middle Deltaic Series. It is less certain how much (if not all) of the Cave, Whitwell and Millepore Oolites may be similarly dated. Certainly there is no evidence in the ostracod fauna to suggest any considerable range in time.

In conclusion, the ostracods, although not giving a very fine correlation between the Yorkshire and Lincolnshire Oolites, substantiate previous stratigraphical correlations. The reason why the ostracods are so uniform throughout the succession is considered to be due to the fact that the Yorkshire and Lincolnshire sediments were deposited during a very short period of time, too short for much evolutionary change to take place. The only apparent evolutionary change appears in the genus *Cytheropterina*. Perhaps one of the more important aspects of the interpretation of the ostracod faunas is to place the topmost beds of the Upper Lincolnshire Limestone below the Grey Limestone Series. Certainly it is doubtful whether the Lincolnshire Limestone as a whole ranges any higher than the *Sonninia sowerbyi* Zone and probably is contained completely within that zone.

APPENDIX

A number of minor sections have been examined which do not appear in the " Stratigraphical Sections " because they are either incomplete or not essential to the stratigraphy of the area. However, a number of ostracod species occur in these minor exposures but not at the same horizon elsewhere. The distribution table (Table 4) would, therefore, be erroneous if they were omitted. A complete faunal list for each of the localities mentioned below is not given, and only those records which extend the stratigraphical range of a species are listed.

1. Upper Limestone—Stonecliff Wood, close to section No. 6, map reference SE/736675 : *Asciocythere acuminata, Eocytheridea* ? *astricta, Eocytheridea faveolata, Systenocythere exilofasciata* and *Systenocythere* ? sp.
2. Millepore Oolite—Osgodby Nab, map reference TA/065855 : *Aulacocythere punctata, Eocytheridea* ? *acuta* and *Eocytheridea reticulata.*
3. Millepore Oolite—Cloughton, map reference TA/021958 : *Cytheropterina plana.*
4. Whitwell Oolite—Bulmer, map reference SE/704678 : *Southcavea grandis.*
5. Kirton Cementstone Series—Kirton Lindsey, map reference SE/942011 : *Pleurocythere kirtonensis.*

V PALAEOGEOGRAPHY

Examination of the ostracod faunas has shown the Lincolnshire Limestone to be of equivalent age to the Yorkshire Oolites and the Hydraulic Limestone/Eller Beck Bed horizon below. Lithologies in some instances remain constant though eventually all become strongly arenaceous and finally completely so when traced northwards.

The environment of deposition of the Lincolnshire Limestone may be treated as a whole. In the Lincoln area the Upper Lincolnshire Limestone is strongly bedded,

OSTRACOD SPECIES	Grey Limeston Series		Basement Beds	Kirton Cementstone Series	Blue and Silver Beds
	polita Zone	*scitu* Zon			
Glyptocythere sp.					
Glyptocythere costata	●				
Glyptocythere polita	●				
Glyptocythere scitula		●			
Malzia bicarinata	●				
Malzia unicarinata	●				
Monoceratina scarboroughensis		●			
Caytonidea faveolata		●			
Cloughtonella rugosa		●			
Fuhrbergiella (Praefuhrbergiella) horrida horrida	●	●			
Progonocythere acuminata	●	●			
Progonocythere yonsnabensis		●			
Pleurocythere sp.		●			
Paracytheridea ? caytonensis		●			
Praeschuleridea subtrigona intermedia	●	●			
Ljubimovella piriformis		●			
Mesocytheridea howardianensis		●			
Southcavea microcellulosa		●			
Systenocythere ovata		●			
Eocytheropteron ? sp.		●			
Vernoniella bajociana		●			
Vernoniella ? caytonensis		●			
Paracypris bajociana		●	●	●	
Cytherella fullonica				●	●
Cytherelloidea catenulata				●	●
Platella jurassica				●	
Bairdia hilda				●	●
Monoceratina vulsa			●	●	
Monoceratina sp. cf. *M. scrobiculata*					
Progonocythere cristata				●	
Acanthocythere (Protoacanthocythere) faveolata			●	●	
Aulacocythere punctata			●	●	
Aulacocythere reticulata					
Fuhrbergiella (Praefuhrbergiella) minima					
Fuhrbergiella (Praefuhrbergiella) arens				●	●
Micropneumatocythere convexa			●	●	
Micropneumatocythere globosa				●	●
Pneumatocythere bajociana			●	●	●
Pneumatocythere carinata				●	
Pleurocythere kirtonensis			●	●	
Pleurocythere nodosa					
Pleurocythere sp.			●		
Dolocythere maculosa			●	●	●
Asciocythere acuminata			●		
Asciocythere lacunosa			●	●	
Eocytheridea ? acuta					
Eocytheridea ? astricta			●		
Eocytheridea carinata					
Eocytheridea elongata			●		
Eocytheridea ? erugata					
Eocytheridea faveolata				●	
Eocytheridea lacunosa			●	●	
Eocytheridea reticulata				●	
Praeschuleridea subtrigona subtrigona				●	●
Praeschuleridea subtrigona magna					
Praeschuleridea ventriosa			●	●	
Cytheropterina comica			●	●	●
Cytheropterina gravis			●	●	●
Cytheropterina plana					
Kirtonella plicata					
Kirtonella reticulata					
Ektyphocythere triangula			●	●	●
Southcavea reticulata				●	
Southcavea bajociana			●		
Southcavea grandis					
Systenocythere exilofasciata			●	●	●
Systenocythere sp.					
Camptocythere lincolnensis				●	●
Cytheromorpha (?) greetwellensis				●	
Cytherelloidea eastfieldensis			●	●	
Progonocythere reticulata			●		
Homocytheridea cylindrica			●		
Tetracytheridea punctata			●		
Paraschuleridea ornata			●		
Paraschuleridea sp.			●		

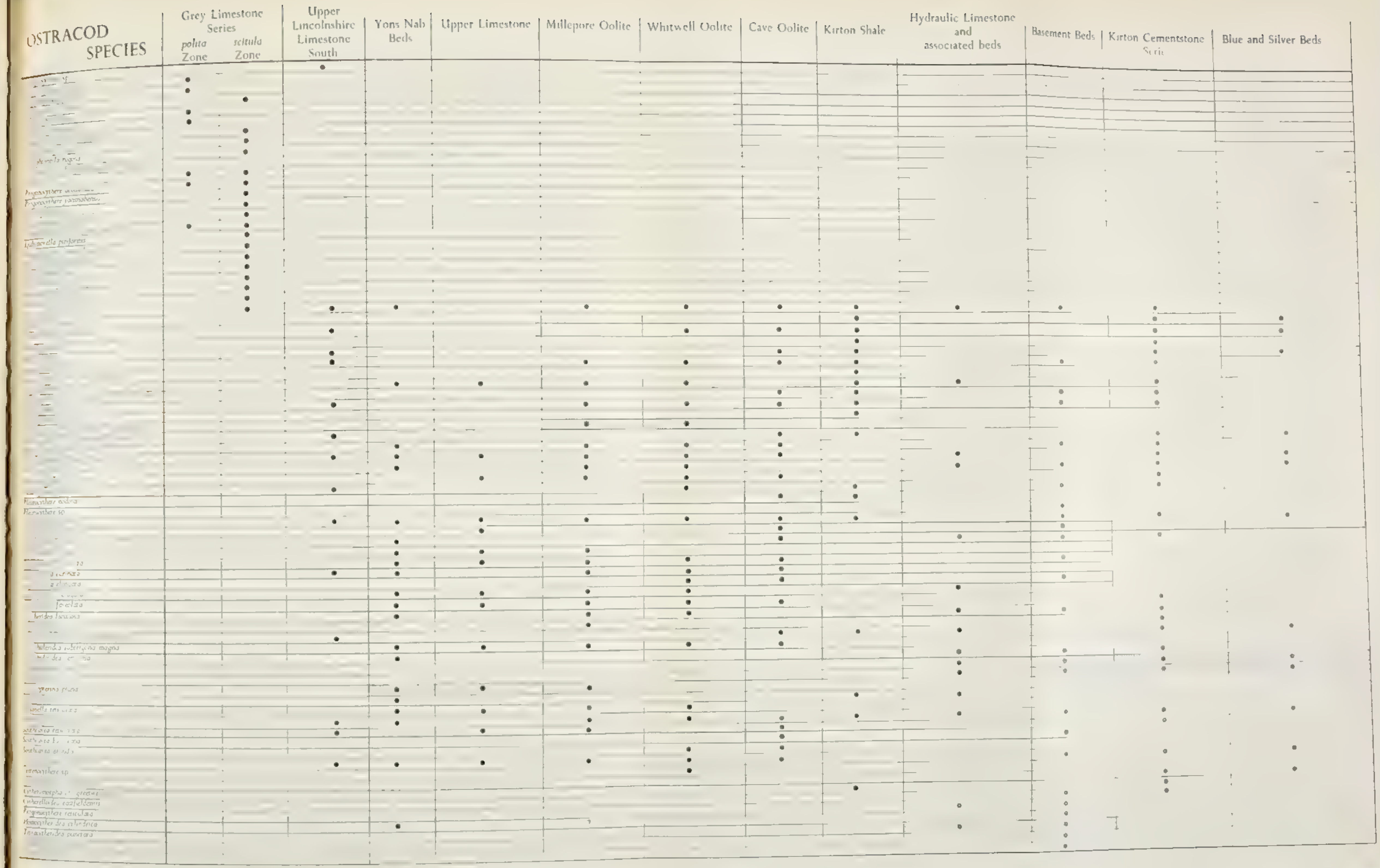

OSTRACOD SPECIES
Grey Limestone Series
polita Zone
scitula Zone
Upper Lincolnshire Limestone South
Yons Nab Beds
Upper Limestone
Millepore Oolite
Whitwell Oolite
Cave Oolite
Kirton Shale
Hydraulic Limestone and associated beds
Basement Beds
Kirton Cementstone Serie
Blue and Silver Beds

TABLE 4. Distribution Chart of Ostracoda within the Bajocian of N.E. England.

often coarsely oolitic. The base of this division, the *A. crossi* Bed, when traced only a few miles to the north becomes a clay-marl, rich in ostracods. The Lower Lincolnshire Limestone on the other hand is fairly stable in this part of its development as a chalky, only poorly oolitic rock with chalky marl bands in the upper part (Cementstone Series) but becomes more massively-bedded and in part coarsely oolitic towards the base (Blue and Silver Beds). Deposition appears to have taken place in warm waters rich in calcium carbonate probably similar to the type of deposition prevalent at the present time in the Bahamas. Current action is not much in evidence at some horizons, particularly during the deposition of the Kirton Shale and the marl bands of the Cementstone Series, and here it is not unusual to find all growth stages in the development of the ostracod retained in the sediment. Current action almost invariably winnows out the smaller instars. Horizons exhibiting oolith formation have experienced some current action, and rolled gastropods, often coated with calcium carbonate, are not uncommon.

All the lithological units of the Lincolnshire Limestone point to deposition in a warm, shallow sea in which chemical precipitation of calcium carbonate was probably high and current action, when present, resulted in the formation of ooliths, again very much like the present-day Bahamas.

To the north of Lincolnshire a fairly large delta, situated in north-east Yorkshire, was discharging into the sea, but had little effect upon the Lincolnshire Limestone as such. This was almost certainly due to the presence in the region of Market Weighton of a stable land barrier (occasionally covered by shallow water) which effectively cut off the Yorkshire Basin from marine deposition to the south. Correlation of the Lincolnshire Limestone with the marine horizons in Yorkshire suggests that if the sea did not transgress over the Market Weighton stable area, then it must have passed around it to the east, the main body of the sea being situated in a similar position to the present-day North Sea.

The Lincolnshire Limestone is represented by two marine horizons in Yorkshire, and it is proposed to deal with these separately.

Hydraulic Limestone/Eller Beck Bed

From Lincoln northwards there is an increase in the marl facies within the Lower Lincolnshire Limestone so that to the north of the Humber marked changes occur. Here, the Cave Oolite is still an oolitic limestone but the beds beneath are predominantly marls (the Basement Beds) with some rubbly limestone and a thin (2 ft. 6 ins.) grey, porcellaneous limestone termed the Hydraulic Limestone. The Lower Estuarine Series beneath may be marine but is no longer exposed. The Hydraulic Limestone and associated marine beds are the northern equivalent of the Lower Lincolnshire Limestone as correlated on the ostracod faunas. The ostracod population here is complete in all stages from juvenile instars to adult carapaces, indicative that deposition during Basement Beds time proceeded in relatively quiet waters with little or no current action.

The Hydraulic Limestone does not appear to have passed over the land barrier north of Market Weighton although this area might well have been submerged under shallow-water, almost littoral conditions at that time. Sandy beds below the Hydraulic Limestone at Acklam to the north provide additional evidence that land was close by.

Marine beds continue to underlie the limestone (section No. 4) until about 2–4 miles north of Whitwell where deltaic sediments of the Lower Deltaic Series appear. This is the southernmost extension of the delta front in the west at this time. Farther north the Hydraulic Limestone (generally 2 ft. 6 ins.–3 ft. 0 ins. in thickness) transgresses over an increased thickness of deltaic sediments. As previously mentioned the limestone is not exposed in the east but has been identified in the Fordon borehole as 4 ft. of cementstone. In the west the Hydraulic Limestone can be traced as far north as Skipton Hill after which it is replaced by the Eller Beck Bed facies of ripple

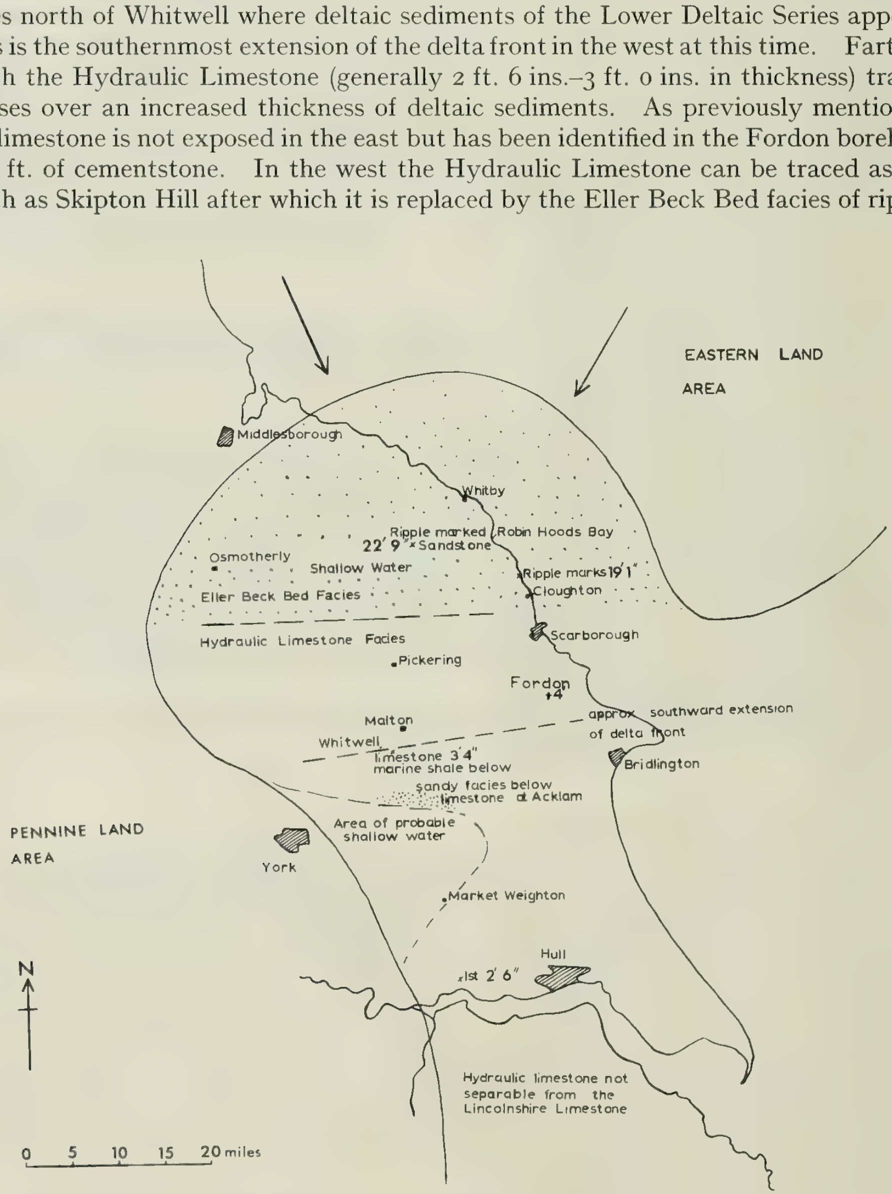

EASTERN LAND AREA
Middlesborough
Whitby
Ripple marked
22' 9" × Sandstone
Robin Hoods Bay
Osmotherly
Shallow Water
Ripple marks 19' 1"
Cloughton
Eller Beck Bed Facies
Scarborough
Hydraulic Limestone Facies
Pickering
Fordon
+4
approx southward extension
of delta front
Malton
Whitwell
limestone 3' 4"
marine shale below
Bridlington
sandy facies below
limestone at Acklam
Area of probable
shallow water
PENNINE LAND AREA
York
Market Weighton
N
Hull
×lst 2' 6"
Hydraulic limestone not
separable from the
Lincolnshire Limestone
0 5 10 15 20 miles

FIG. 4. Palaeogeographic map of the Hydraulic Limestone/Eller Beck Bed marine transgression.

marked sandstone and fossiliferous ironstone bands. This marked change in facies indicates the closeness of the delta front and the shallowness of the water is further indicated by the presence of ripple markings and worm burrows. The considerable increase in the thickness of this marine bed from the Hydraulic Limestone is due to the vast quantity of marine deposited, arenaceous material brought into the area by the northern delta. The absence of a marine fauna in the sandstone is probably due to rapid deposition, always an unsuitable environment for benthonic organisms. Text-fig. 4 indicates the probable palaeogeographic conditions under which the Hydraulic Limestone and the Eller Beck Bed were deposited, open sea being to the south-east.

Deltaic Series

In discussing the marine horizons which transgressed the deltaic sediments it is impossible to get a clear idea as to palaeogeography without also considering the deltaic sediments themselves. I do not propose to go into details of the subdivision of the Series but rather to give general views on their deposition and source.

Prior to 1924 this vast thickness of false bedded sandstones, shales with thin coal seams and important plant beds had been considered estuarine in origin, being so-called by Fox-Strangways (1880). Kendall & Wroot (1924 : 309) were the first to recognize their true deltaic origin, later confirmed by Black (1928, 1929, 1934).

The features which confirm the deltaic nature of these beds are : false bedding (here mainly topset), washouts (especially common in Upper Deltaic Series in Cayton Bay and postulated at Osgodby Nab in the Middle Deltaic Series), beds of *Equisetites* and coal seams. The burnt bed in the Lower Deltaic Series represents an old forest fire. The *Equisetites* grew in swamps behind the advancing delta front whilst the more substantial trees grew further back.

Deposition of these deltaic sediments took place in a gently subsiding basin with a Pennine land mass to the west, a partial land barrier to the south at Market Weighton and possibly land to the north and north-east. Open sea lay to the south-east. There is some difference of opinion as to whether land was present to the north and whether the source of the deltaic sediments lay in that direction or to the east.

Black (1934 : 279) considered the Yorkshire basin to be in a south-western angle of a gulf opening to the north with derivation of sediment from the east. He did not believe that the Pennine land supplied much material, a conclusion with which I agree. Black also stated that the emergent land in the Market Weighton area formed a barrier and that the mineral suites differ so remarkably to the north and south that they must have been derived from different sources. Smithson (1942) came to a similar conclusion with regard to the mineral suite but did not follow Black in deriving the sediments from the east and considered the main source to have been from the north-north-west. This was confirmed by a grain size study, especially of zircon, which gave this same constant direction of incoming material for both deltaic and marine sediments. Sorby (*in* Fox-Strangways, 1892 : 391) was also of the opinion that the drift-bedding and ripple marks were produced by north-north-westerly currents. The findings of Sorby and Smithson are accepted here.

Correlation of the Lincolnshire Limestone with the marine horizons in Yorkshire indicates that the marine transgression came from the south-east and skirted around the Market Weighton barrier. The marine beds deposited during the transgression die out northwards against the delta, in which direction land obviously lay. Smithson also considered land to be present to the east. The increase in arenaceous sediments to the north-east in particular would suggest that land certainly lay in that direction, as indicated in the palaeogeographic interpretations of the Hydraulic Limestone and of the Millepore and Whitwell Oolites. Derivation of the deltaic sediments in Yorkshire is thus considered to have been mainly from the north-west with subsidiary material from the north-east. The Pennine land to the west and the Market Weighton land to the south represent the coastline of the bay. The land-derived material in the Lincolnshire basin is not dominant in the limestone facies and was possibly derived from the Pennine land to the west and/or the London–Ardennes island to the south.

Millepore and Whitwell Oolites

For a time the Yorkshire basin was filled by deltaic sediments of the Middle Deltaic Series until further subsidence produced another marine transgression, much more prominent than that which formed the thin Hydraulic Limestone and the poorly-fossiliferous Eller Beck Bed. The Whitwell Oolite in the west is perhaps the better developed and, apart from the rather sandy beds overlying it, does not contain a large proportion of arenaceous material until traced northwards. Although a Pennine land mass must have been present to the west it did not supply much material compared with conditions farther north. In the west and south-west the present-day outcrop represents a shallow water deposit close to a land mass which did not have large rivers bringing in material, the sand being more of a shore-line deposit. Shallow-water conditions may have covered the land barrier in the Market Weighton area though there was little connection between the Yorkshire sediments and those just north of the Humber. The reasons for this are based to some extent on faunal evidence. *Praeschuleridea subtrigona magna* was virtually restricted to the Yorkshire basin and is regarded as a geographic subspecies ; only a few specimens have been recorded from the Cave Oolite and none from the Lincolnshire Limestone. The marine *Bairdia hilda* does not occur north of Market Weighton where the effect of the delta might have lowered the salinity to some extent, although *Paracypris bajociana*, also regarded as a good marine ostracod, is common. Within the Yorkshire basin there is also a preponderance of species of *Eocytheridea*, some of which have not been recorded from Lincolnshire. This may also be due to ecological conditions in the vicinity of the delta.

Farther east, away from the western land mass, the Millepore Oolite as exposed in Cayton Bay exhibits strong false-bedding and current action must have been fairly strong in that region. When traced northwards both the Whitwell and the Millepore Oolites become more arenaceous until they are finally indistinguishable from a typical deltaic sandstone. The delta front has been reached. The uppermost beds of the Whitwell Oolite are known as the Upper Limestone and those of the

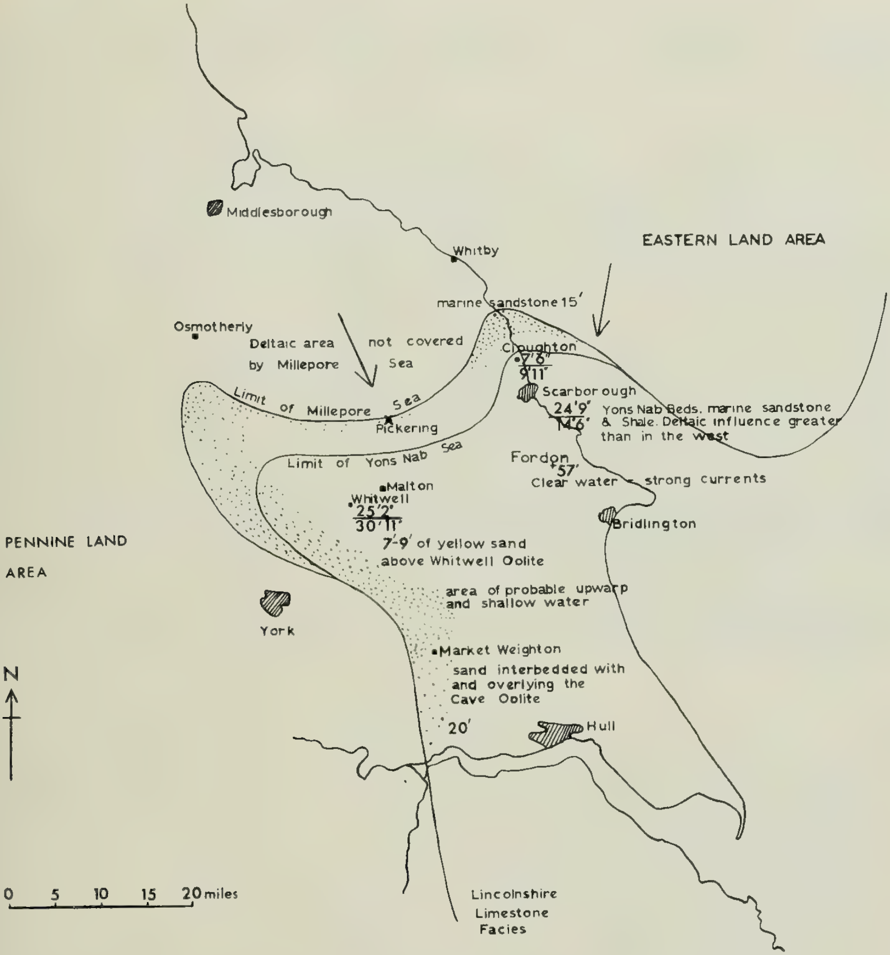

Middlesborough
Whitby
EASTERN LAND AREA
marine sandstone 15′
Osmotherly
Deltaic area not covered by Millepore Sea
Cloughton
7′6″
9′11″
Scarborough
24′9″
14′6″
Yons Nab Beds, marine sandstone & Shale. Deltaic influence greater than in the west
Limit of Millepore Sea
Pickering
Limit of Yons Nab Sea
Fordon
57′
Clear water – strong currents
Malton
Whitwell
25′2″
30′11″
Bridlington
PENNINE LAND AREA
7′-9′ of yellow sand above Whitwell Oolite
area of probable upwarp and shallow water
York
Market Weighton
sand interbedded with and overlying the Cave Oolite
N
20′
Hull
0 5 10 15 20 miles
Lincolnshire Limestone Facies

FIG. 5. Palaeogeographic map of the Millepore/Whitwell Oolite marine transgression.

Millepore Oolite as the Yons Nab Beds. The former is a siliceous limestone whilst the latter tends to be a shale/sandstone sequence. These higher beds represent the final stages in the marine transgression and do not extend as far north as the main marine transgression represented by the oolites beneath. The Yons Nab Beds are close to the delta front throughout their exposed development. The palaeogeographic interpretation of this marine episode illustrated in Text-fig. 5 is closely comparable to Smithson's (1942, fig. 15).

Conclusions

The land barrier in the vicinity of Market Weighton represented a stable area between subsiding basins to the south and the north.

The southern basin was infilled with calcareous sediments (the Lincolnshire Limestone) deposited in lime rich waters. The Pennine land to the west and the London-Ardennes Island to the south did not supply a large quantity of terrigenous material.

The northern basin, on the other hand, received a considerable amount of terrigenous material from its northern boundaries in the form of deltaic sediments. The Yorkshire delta was quite substantial and had a considerable effect upon sedimentation although this was limited to Yorkshire. Open sea lay to the south-east and it was from this direction that the sea entered to transgress the Yorkshire delta on two separate occasions during the continuous deposition of the Lincolnshire Limestone farther south.

The first transgression gave rise to the Hydraulic Limestone and the Eller Beck Bed and took place in Lower Lincolnshire Limestone times. A period of deltaic sedimentation separates this transgression from the second marine incursion during which the Whitwell Oolite and associated Upper Limestone and the Millepore Oolite and Yons Nab Beds were deposited. This second transgression occurred in Upper Lincolnshire Limestone times. Both incursions came from the south-east.

During Middle Jurassic times a third marine transgression covered the Yorkshire delta and was responsible for the Grey Limestone Series (Bate 1965). The sea did not enter from the south-east, but came directly from the east, indications being that land lay to the south, probably in Lincolnshire where no marine deposition would have taken place at that time.

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FURTHER NOTES ON PALAEONISCOID FISHES WITH A CLASSIFICATION OF THE CHONDROSTEI

BY

BRIAN GEORGE GARDINER, Ph.D.
(Queen Elizabeth College, University of London)

Pp. 143–206 ; 3 *Plates* ; 24 *Text-figures*

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By B. G. GARDINER

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SYNOPSIS

A redescription is given of the type species of the genera *Gonatodus* Traquair, *Drydenius* Traquair, *Sphaerolepis* Frič, *Sceletophorus* Frič and *Phanerorhynchus* Gill. *Pseudogonatodus gen. nov.* is proposed for two species previously placed in *Gonatodus*. Eight new palaeoniscoid families are erected, the Gonatodidae, Osorioichthyidae, Gyrolepidotidae, Atherstoniidae, Lawniidae, Cosmolepididae, Brachydegmidae and Boreosomidae. One other new chondrostean family is proposed, the Habroichthyidae which belongs to the order Peltopleuriformes. The evolution of the Chondrostei is discussed and a classification of the Subclass given.

I. INTRODUCTION

Traquair (1877–1914), in his monograph on " The Ganoid fishes of the British Carboniferous formations ", described the majority of the palaeoniscoids occurring in our Carboniferous strata. Subsequently Moy-Thomas and Dyne (1938) re-described and supplemented that portion of the fauna which occurred in the Lower Carboniferous rocks of Glencartholm. In an earlier paper (Gardiner 1963) I began the task of revising all the genera described by Traquair (1877–1914) except those adequately dealt with by Moy-Thomas & Dyne (1938) and this paper is intended to be a continuation of that work. In addition to genera described by Traquair I have redefined the Upper Carboniferous genus *Phanerorhynchus* Gill and redescribed two genera from the Upper Carboniferous of Czechoslovakia, *Sphaerolepis* Frič and *Sceletophorus* Frič.

Having examined almost all the palaeoniscoids, I have attempted a classification of the Palaeonisciformes, and, treated the much bigger problem of the evolution of the Chondrostei and its classification.

Later I hope to redescribe *Cryphiolepis* Traquair, *Acrolepis* Agassiz, *Myriolepis* Egerton and *Styracopterus* Traquair and then, in order to complete the survey, all the many species which were dealt with by Traquair will be re-examined in the light of my emended generic diagnoses.

II. SYSTEMATIC DESCRIPTIONS

Order **PALAEONISCIFORMES**

Family **GONATODIDAE** nov.

Diagnosis. Trunk deeply fusiform ; dorsal fin situated behind the middle of the back, more posterior in position than in *Elonichthys* Giebel. The remaining diagnosis as for the genus *Gonatodus*.

Remarks. From my description of *Gonatodus* it is clear that this genus does not belong in the Family Elonichthyidae where both Romer (1945 : 579) and Obruchev (1964 : 352) placed it ; further it does not fit into any other previously described family. A new family, Gonatodidae, is therefore erected to include this genus and the related genera *Drydenius* Traquair and *Pseudogonatodus* nov. The Gonatodidae later gave rise to both the Commentryidae Gardiner (1963 : 290) and the Amblypteridae Romer (Gardiner 1963 : 290).

Genus ***GONATODUS*** Traquair, 1877

1835 *Amblypterus* Agassiz (*partim*) **2**, 1 : 109.

Diagnosis (emended). Trunk deeply fusiform ; dorsal fin situated behind middle of back, partly in advance of, partly opposing, anal, both being large, triangular and approximately the same size. Dorsal contour arched in advance of dorsal fin. Paired fins large, pelvic pair midway between pectorals and anal. All fins with minute fulcra anteriorly and with rays closely articulated, so as to impart scale-like appearance to individual joints ; all rays distally bifurcated. Skull with suspensorium somewhat inclined, not so near vertical as in *Amblypterus*, moderately overhanging rostrum and relatively stout sclerotic ring. Opercular more than twice as deep as subopercular; suborbital series and dermohyal present. Branchiostegal rays numerous, skull roofing bones coarsely striated. Teeth closely set, of moderate size and in one series. Scales large with distinct peg and socket articulation, and ornamented with fine, oblique striae.

TYPE SPECIES. *Amblypterus punctatus* Agassiz.

REMARKS. Agassiz (1835, **2**, 1 : 109) in describing [the new species] *Amblypterus punctatus* used three specimens (R.S.M. 1878.18.4, R.S.M. 1878.18.6 and one in the Oxford University Museum) all of which are from the Calciferous Sandstone Series (Lower Carboniferous) of Wardie. Traquair (1877 : 265 ; 1877*b* : 555 ; 1877*c* : 60) realized that the species *Amblypterus punctatus* Agassiz was founded not only on two distinct species but that each of the two species belonged to different genera. For one of Agassiz's original syntypes (R.S.M. 1878.18.4) Traquair (1877) retained the specific name "*punctatus*" and used it to form the type of the new genus *Gonatodus*. To the other two syntypes of Agassiz (1835, **2**, 1, pl. 4*c*, figs. 3, 5) Traquair gave the new specific name *Elonichthys intermedius*. Traquair (1901 : 67) decided that *Elonichthys intermedius* was merely a variation of *Elonichthys robisoni* (Hibbert), and called it *Elonichthys robisoni* Hibbert var. *intermedius* Traquair. From an examination of the type material it is clear that Traquair was justified in separating the syntypes of Agassiz's *Amblypterus punctatus* into the two distinct species, *Gonatodus punctatus* (Agassiz) and *Elonichthys robisoni* (Hibbert).

The genus contains but the type species, the other two species referred to it by Traquair (1907), *Gonatodus parvidens* Traquair and *Gonatodus macrolepis* Traquair, are placed in a new genus, *Pseudogonatodus*.

Two other species that have in the past been included in this genus, *Gonatodus brainerdi* (Newberry 1873 : 346 ; 1890 : 125) and *Gonatodus ? toilliezi* (Koninck 1878 : 11), clearly belong elsewhere as already indicated by Traquair (1907 : 93). *Gonatodus brainerdi* from the Berea Grit of Ohio (Lower Carboniferous) is from its large size possibly a *Nematoptychius* ; while *Gonatodus ? toilliezi* from the Lower Carboniferous of Viesville, Belgium, has large fulcra and seems closer to *Canobius* than to *Gonatodus*.

Gonatodus punctatus (Agassiz)

(Text-figs. 1–4)

1835 *Amblypterus punctatus* Agassiz, **2**, 1 : 109, pl. 4*c*, fig. 4 (non figs. 3, 5–8).
1872 *Amblypterus anconoaechmodus* Walker : 119, pl. 1.
1877 *Gonatodus punctatus* (Agassiz) Traquair : 265.
1877*b* *Gonatodus punctatus* (Agassiz) ; Traquair : 555.
1877*c* *Gonatodus punctatus* (Agassiz) ; Traquair : 16, 60, pl. 2, figs. 4, 5.
1882 *Gonatodus punctatus* (Agassiz) ; Traquair : 546.
1890 *Gonatodus punctatus* (Agassiz) ; Traquair : 391.
1891 *Gonatodus punctatus* (Agassiz) ; Woodward : 434.
1903 *Gonatodus punctatus* (Agassiz) ; Traquair : 690, 700, 701.
1907 *Gonatodus punctatus* (Agassiz) ; Traquair : 93, pl. 19, text-figs. 2, 3*a*.
1907*b* *Gonatodus punctatus* (Agassiz) ; Traquair : 106, 114, 115, pl. 2, figs. 1, 2.
1925 *Gonatodus punctatus* (Agassiz) ; Watson : 859, text-fig. 27.
1954 *Gonatodus punctatus* (Agassiz) ; Waterston : 58.

DIAGNOSIS (emended). Fishes not exceeding 18·5 cm. in total length, body deeply fusiform, length of head contained slightly more than three and a half times and depth of body about two and three-quarter times in total body length (measured to bifurcation of caudal fin). Head short with bluntly rounded snout. Skull with two dermohyals, and teeth on jaws arranged in single closely set row. Scales of moderate size deeper than broad on flank and ornamented with distinct concentric ridges of enamel imparting delicate serration to posterior margin. Many ridges on dorso-posterior region of scales short and terminating in points before posterior margin is reached (Text-fig. 3).

HOLOTYPE. R.S.M. 1878.18.4, head and anterior half of fish wanting fins, from the Calciferous Sandstone Series (Lower Carboniferous) of Wardie, Edinburgh.

MATERIAL. In addition to the holotype, five complete fish, three tolerably complete fish, five skulls, isolated maxillae and scales in the British Museum (Natural History) and the Royal Scottish Museum, Edinburgh.

REMARKS. The specific name *punctatus* is rather an unfortunate one since the normal scale ornamentation consists of quite distinct, characteristic ridges of enamel. Only the occasional specimen has scales which show coarse punctures over the exter-

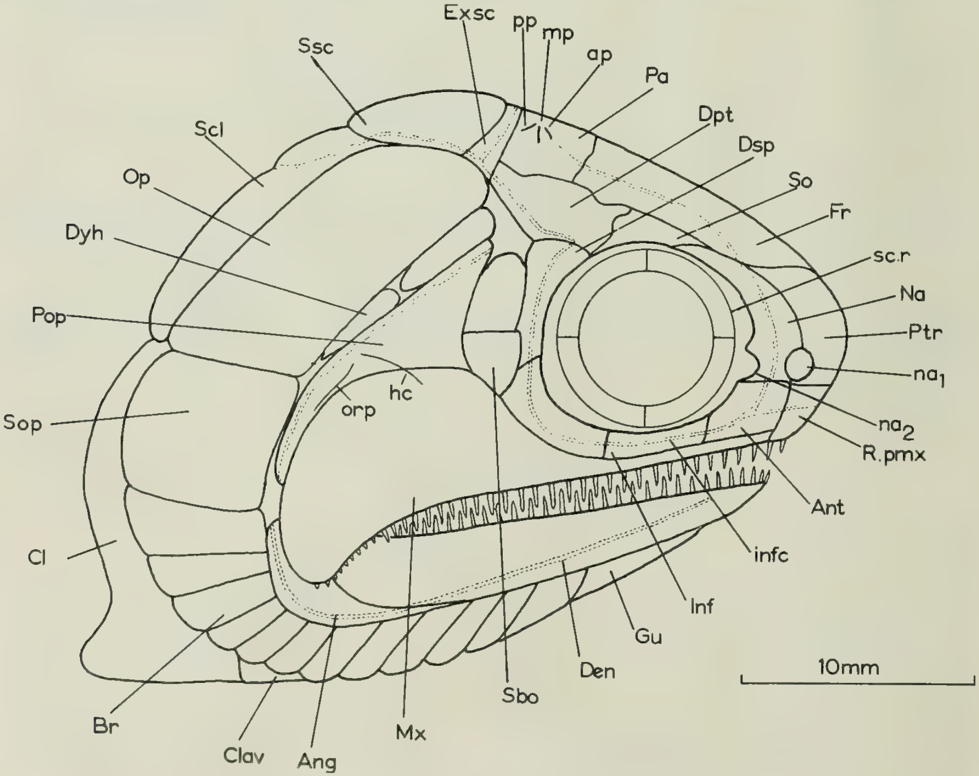

FIG. 1. *Gonatodus punctatus* (Agassiz). Reconstruction of skull in lateral view.

nal surface, and in these cases it is due to the resorption of most of the enamel layer, so that one is merely looking at the deeper layers of the scale, the punctures representing old blood vessel pathways.

I have already discussed the loss of ornamentation in the genus *Namaichthys* (Gardiner 1962 : 19) but without really emphasizing this process of resorption. Resorption has been noted in the Agnatha, the Dipnoi and the Crossopterygii, in skull roofing elements as well as scales, but has not so far been noticed in the Actinopterygii. Resorption of the scale ornamentation is most marked in the genus *Elonichthys* (*E. robisoni* (Hibbert), *E. semistriatus* Traquair) but I have also observed it in *Rhadinichthys*, *Drydenius* and *Gonatodus*. Normally the ornamentation of the scales in the posterior region is the first to undergo resorption, thus often the anterior part of the fish shows scales with a complex ornamentation of ridges and striae of enamel while the posterior scales are smooth apart from a distinct puncturing. In the past when the erection of species on scale ornamentation was a common practice this led to the naming of species which can often now be shown to be merely differences in resorption of an original scale type.

The scales from Wardie figured by Traquair (1901, pl. 9, figs. 6, 7) as *Elonichthys robisoni* (Hibbert) var. *intermedius* Traquair are identical with those of *Gonatodus punctatus* (Agassiz). Traquair believed that the sculpturing exhibited by these scales was due to the loss of the ganoine (enamel) layer. However, it is now clear that these figures of Traquair's (pl. 9, figs. 6, 7) represent the normal, ornamented, external scale surface of *Gonatodus punctatus*.

DESCRIPTION. *The skull.* The general shape of the skull can be seen from Text-fig. 1. Although the snout has a distinct rostrum, it is not nearly so pronounced as in the genera *Elonichthys* Giebel and *Nematoptychius* Traquair. The most characteristic features are the dermohyals and the arrangement and shape of the teeth.

The skull roofing bones are all ornamented with stout ridges of enamel, which in places give way to tubercles. On the parietals, frontals, dermopterotics and postrostral bones the ridges are broken up into elongated tubercles which run from the centre of ossification outwards. The ridges of enamel on the suprascapulars and extrascapulars are in the form of short striae which run concentrically. A similar ornamentation is seen on the suborbitals. The maxilla is covered by long ridges of enamel, partially broken up into segments, which sweep up and round the bone, running parallel with its posterior and superior borders. Ventrally the maxilla has more tubercles. On the subopercular the ridges are short and run more or less parallel horizontally, while on the opercular they are also short but run diagonally across the bone from the antero-dorsal corner.

The mandible is covered by long straight ridges of enamel which run along its entire length, a similar condition is seen on the branchiostegal rays, except that the ridges are much fewer in number.

The skull is relatively short and the suspensorium not too far off the vertical. The suprascapulars are broad and meet in the midline and the extrascapular series consists of the normal narrow, single pair of bones. The paired parietals are rectangular while the frontals are the longest bones in the skull roof and anteriorly meet both the postrostral and nasals. Laterally the frontal is bordered by the dermopterotic, supraorbital and nasal.

The lateral roof of the skull is comprised of two bones, the dermopterotic and the supraorbital. The dermopterotic is the larger and its dorsal margin is strongly emarginated at two points. Anteriorly the dermopterotic joins the shorter supraorbital, which separates it from the nasal. The nasal is short and broad and its lateral margin forms together with the dorsal margin of the antorbital a distinct notch, which indicates the position of the posterior nostril. The anterior nostril lies between the nasal and the postrostral. Posteriorly the nasal joins the frontal and supraorbital. The postrostral is another stout, broad bone, moderately convex anteriorly, which meets ventrally the paired, toothed, rostro-premaxillaries. Posterior to the rostro-premaxillary is a stout antorbital, which does not enter into the jaw margin.

There are two members of the infraorbital series while the dermosphenotic is long and forms a considerable portion of the upper posterior margin of the orbit. The suborbital series consists of two rounded bones, the upper of which is the larger.

The maxilla is of the normal palaeoniscoid pattern and curves slightly upwards before it meets the rostro-premaxillary. The ventral margin bears teeth along its entire length ; the teeth are nearly uniform, long and stout and arranged in a single closely set row. Each tooth has a distinct terminal cap. The preopercular is a high bone with its posterior margin much nearer to the vertical than that of *Elonichthys*. Behind the preopercular and filling the gap between it and the opercular lie two wedge-shaped dermohyals. However in one specimen, R.S.M. 1926.57.16, at least three dermohyal elements are present. The opercular is rectangular in outline and more than twice as high as the subopercular. Preceding the subopercular are twelve to thirteen broad branchiostegal rays and a large median gular. The orbit is supported by a stout sclerotic ring composed of four elements.

The lower jaw. Posteriorly the lower jaw is much deepened due to the upward extension of the dentary and to the presence of a surangular, much as in *Amblypterus*. The outer surface of the jaw is formed by a stout angular posteriorly while the remainder is made up of the large dentary. The dentary also forms part of the inner surface anteriorly. The remainder of the inner surface is covered by a large prearticular. The upper border of the dentary supports a single series of stout, tall, rather closely set teeth. There is a coronoid series which overlaps the dorsal, internal portion of the dentary. Posteriorly the articular portion of Meckel's cartilage is ossified.

The palate. The palate has already been figured by Watson (1925, text-fig. 27). The quadrate is stout and the ectopterygoid small in comparison with the much longer entopterygoid. The metapterygoid is well ossified as is the remainder of the suprapterygoid series which forms a single, large ossification. Anteriorly the suprapterygoid is notched for the passage of the maxillary and mandibular divisions of the fifth nerve. The palatine is a mere sliver of bone, but both it and the ectopterygoid bear a single row of large teeth. Anteriorly there is a pair of toothed vomers.

The neurocranium. Apart from the parasphenoid, little can be made out. The

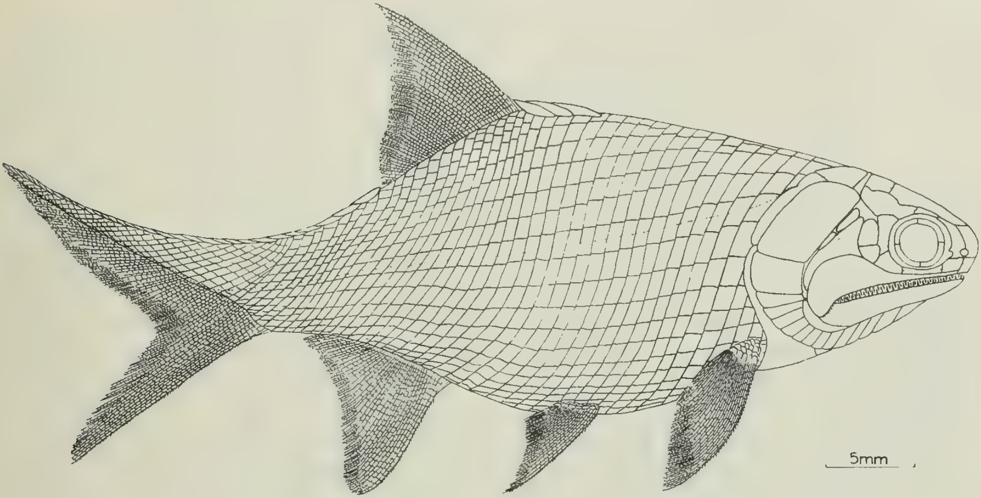

FIG. 2. *Gonatodus punctatus* (Agassiz). Restoration of whole fish.

parasphenoid is short and broad as in *Pteronisculus* White, with a well marked basipterygoid process (see Traquair 1877*c*, pl. 2, fig. 5).

The paired fins and their girdles. The pectoral girdle consists of a supracleithrum which stretches down to the junction between the opercular and subopercular, an elongate cleithrum and a stout clavicle.

The ornamentation on the supracleithrum is delicate, with ridges of enamel which branch to a limited degree and run across the bone rather than following its length as they do on the cleithrum.

The pectoral fin is large with between thirty and thirty-two lepidotrichia. The rays are smooth and the articulations tolerably close, especially in the finer rays of the posterior part of the fin. However, in the most anterior fin rays the articulations are quite far apart. The base of the fin is covered by a series of small scales.

The pelvic fin is somewhat smaller with between eighteen and twenty rays, all closely articulated.

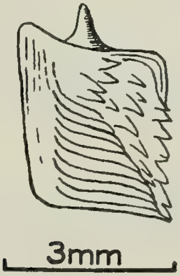

FIG. 3. *Gonatodus punctatus* (Agassiz). Anterior flank scale.

The unpaired fins. Both dorsal and anal fins are triangular and of similar size with between forty and forty-five rays. The articulations of the rays in both fins are so close that the joints of the base of the fins look most scale-like. The fin rays are smooth apart from a single longitudinal furrow.

The caudal fin is heterocercal, inequilobate and deeply cleft.

The squamation. The scales of the flank are slightly higher than broad and at the deepest point of the body number around twenty-two rows. They possess a distinct peg and socket articulation and in proportion to body size the scales are large. The ornamentation is most distinct consisting of prominent ridges of enamel (Text-fig. 3). The ridges follow the postero-ventral margin and also the dorsal margin. There is a triangular portion posteriorly where short, pointed, overlapping tubercles pass back towards the hind margin which is pectinated.

There are three large ridge scales in front of the dorsal fin, and the ridge scales of the axial lobe start immediately behind the dorsal fin.

Scale structure. The general structure of the scale can be seen from Text-fig. 4. Aldinger (1937 : 212) has already pointed out the similarity of the scale structure to that seen in *Elonichthys*. The canal plexus of the dentine layer is composed of horizontal and radial canals (vascular). The horizontal canals bear tree-like dentine tubules. The radial canals penetrate obliquely through the bony lamellae from the scale margins, sending feeder branches upwards to connect with the horizontal canals. Thus the radial canals are for the most part at a much deeper level than the horizontal canals. A few canals (canals of Williamson) penetrate upwards from the centre of the base of the scale to connect with both the radial canals and the horizontal canals. The horizontal canals often connect with one another by means of radial cross connections. Occasionally ascending branches of the dentine canal plexus penetrate the external enamel layer (as in *Elonichthys*). Bone cells are present in the bony lamellae but no fibres of Sharpey were observed.

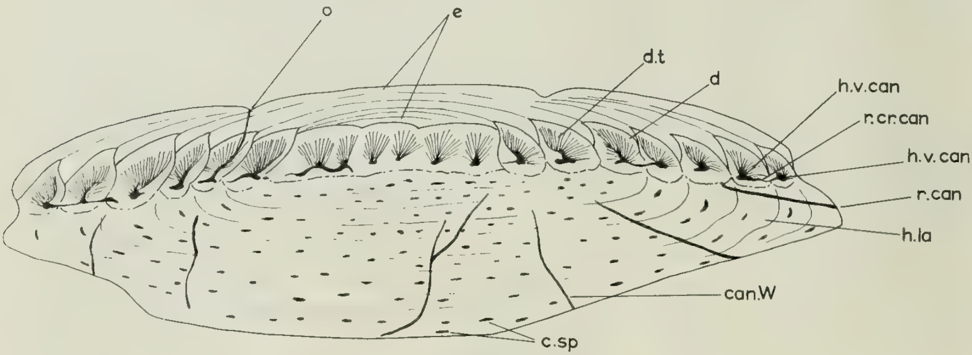

FIG. 4. *Gonatodus punctatus* (Agassiz). Dorso-ventral cross section through mid-lateral scale. ×45. From B.M.N.H. P.11704.

In overall structure the scale of *Gonatodus punctatus* is close to that of *Elonichthys*.

Locality and horizon. Apparently confined to the Calciferous Sandstone Series (Lower and Middle Visean) at the base of the Scottish Lower Carboniferous. It is recorded from ironstone nodules at Wardie, Edinburgh, from Gullane, East Lothian and from Pitchorthy, Fifeshire. One specimen, also in an ironstone nodule, is recorded from Collinton, Edinburgh (B.M.N.H. P.11704).

Genus ***PSEUDOGONATODUS*** nov.

1877 *Gonatodus* Traquair (*partim*) : 271.
1882 *Gonatodus* Traquair (*partim*) : 546.

Diagnosis. Body fusiform ; dorsal fin placed rather far back (nearer to tail than in *Gonatodus* Traquair), partly in advance of, partly opposing the anal but giving appearance of being almost opposite it. Both fins of moderate size, triangular, smaller than in *Gonatodus*. Paired fins large, with stout rays, pelvics placed nearer to anal than to pectorals ; caudal fin deeply cleft and inequilobate. All fins with prominent fulcra anteriorly and rays closely articulated and distally bifurcated. Skull with almost vertical suspensorium (as in *Amblypterus*) and rostrum not pronounced. Opercular less than one and three-quarter times as deep as subopercular. Suborbital and dermohyal series present. Branchiostegal rays numerous, skull roofing bones and cheek bones ornamented with coarse, stout ridges of enamel ; teeth of variable size but in single series. Scales rhomboid and large (larger than in *Gonatodus*), ornamented with fine striae and distinct punctations.

Type species. *Gonatodus parvidens* Traquair.

Remarks. Traquair (1877 ; 1882) placed three species in the genus *Gonatodus*, *G. punctatus* (Agassiz), *G. macrolepis* Traquair and *G. parvidens* Traquair. It is now clear that *G. parvidens* and *G. macrolepis* are not congeneric with *G. punctatus* and the new genus *Pseudogonatodus* is here proposed for them. For the type species I have selected *G. parvidens* since this is by far the better known of the two species.

Pseudogonatodus parvidens (Traquair)

(Text-figs. 5, 6)

1881 *Gonatodus* sp., Traquair : 315 (name only)
1882 *Gonatodus parvidens* Traquair : 546.
1890 *Gonatodus parvidens* Traquair ; Traquair : 392.
1891 *Gonatodus parvidens* Traquair ; Woodward : 435, pl. 16, fig. 7.
1903 *Gonatodus parvidens* Traquair ; Traquair : 695, 696, 700, 701.
1907 *Gonatodus parvidens* Traquair ; Traquair : 99, pl. 21, text-fig. 3*c*.
1937 *Gonatodus parvidens* Traquair ; Aldinger : 212, text-fig. 55.
1954 *Gonatodus parvidens* Traquair ; Waterston : 57.

Diagnosis (emended). Fishes not exceeding 22 cm. in total length, body fusiform, length of head contained little over five times and greatest depth of body four times in total body length. Suspensorium nearly vertical, head short and with bluntly rounded snout. Maxilla of distinctive shape, high posteriorly. Single large suborbital present. Teeth on jaws very small, arranged in single closely-set row.

Scales large in proportion to body size, deeper than broad on the flank, feebly ornamented with few striae and exhibiting coarse punctations. Posterior borders of scales delicately serrated.

Lectotype, here chosen. R.S.M. 1926.57.19, a tolerably entire fish from the Borough Lee Ironstone, Edge Coal series, Loanhead, near Edinburgh.

Material. In addition to the lectotype, about twelve almost complete fish, eight bodies wanting skull, two skulls, isolated maxillae, scales and jaws in the British Museum (Natural History) and the Royal Scottish Museum, Edinburgh.

Remarks. *Pseudogonatodus parvidens* (Traquair) was first recognized by Traquair (1882 : 546) as a distinct species using detached maxillary bones from the Borough Lee Ironstone supplemented by more or less entire fish from the same locality. The

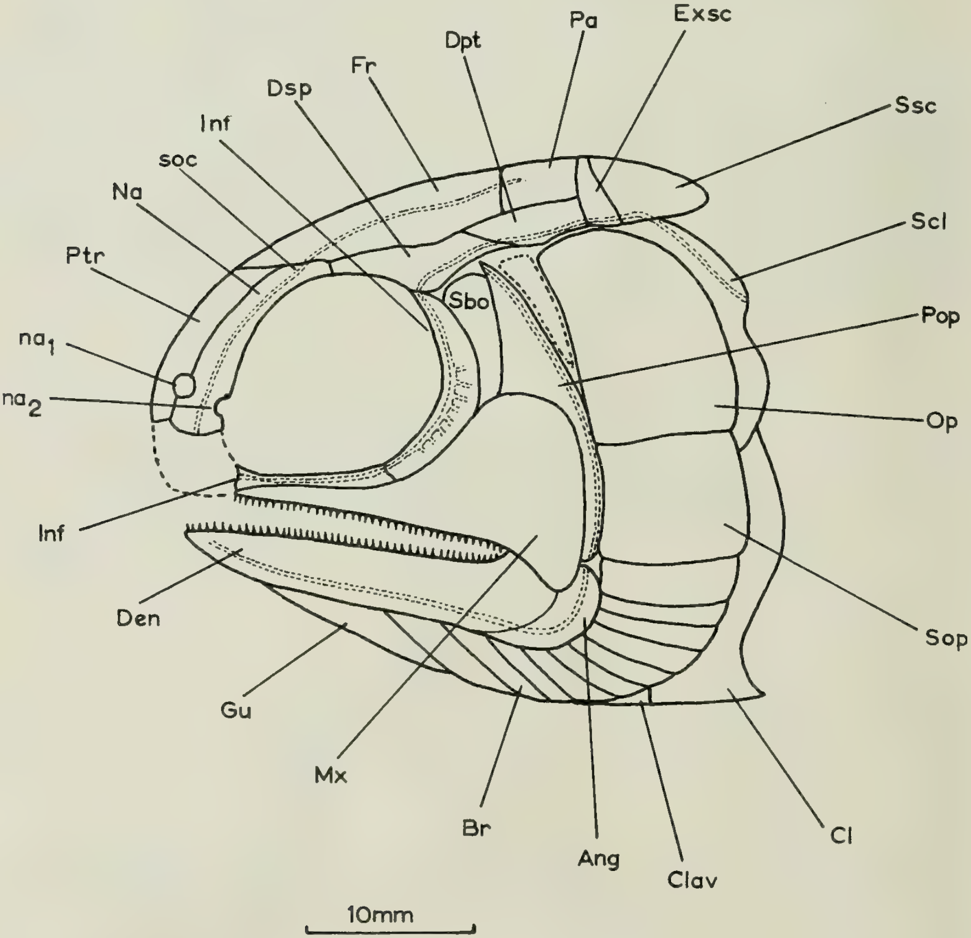

Fig. 5. *Pseudogonatodus parvidens* (Traquair). Reconstruction of skull in lateral view.

maxilla is perhaps still the most characteristic feature by which the species can be recognized.

The ornamentation of the scales, with few striae and many punctations, is misleading and is once more the result of resorption of superficial enamel. It would seem that if younger, better preserved specimens were available a more extensive ornamentation comprising ridges of enamel would be apparent.

DESCRIPTION. *The skull.* The bones of the skull and course of the sensory canals are shown in Text-fig. 5. The more distinctive features are the almost upright suspensorium and the shape of the maxilla.

The skull roofing bones are all ornamented with stout, long ridges of enamel, more pronounced than in *G. punctatus*. The ridges more or less follow the length of the bones with a few interspersed tubercles on the frontals and the anterior end of the postrostral. The ridges on the maxilla are likewise prominent, running up and round the bone parallel with the posterior and superior borders. Even on the anterior end of the maxilla short ridges run upwards from the ventral surface. On the subopercular the ridges run parallel from front to back while on the opercular they run diagonally across from the antero-dorsal corner. On the mandible the ridges of enamel are again stout and run along its entire length. Similarly on the gular plate and branchiostegal rays stout long striae run along the long axis of the bones.

The skull is short and the suspensorium almost upright (nearer the vertical than in *Gonatodus*). The suprascapulars are of normal size and are preceded by a narrow pair of extrascapulars. The parietals are square in outline and the frontals are very large. Anteriorly the frontal meets both postrostral and nasal. Laterally the parietals and frontals are bordered by the dermopterotic and dermosphenotic. The dermopterotic is roughly rectangular but anteriorly is produced into a point. The dermosphenotic is larger than the dermopterotic and anteriorly meets the nasal. Both the nasal and the postrostral are long, stout bones of somewhat the same proportions as in *Amblypterus*. The position of the anterior nostril is clearly marked between the postrostral and nasal while that of the posterior is indicated by a distinct notch in the nasal. Both nostrils are borne rather high up on the snout as in *Amblypterus*. The most anterior portion of the snout is not clearly preserved in any of the specimens I have examined.

There are two members of the infraorbital series, the second of which is much expanded. The infraorbital sensory canal on its passage through this second infraorbital gives off many short branches posteriorly. The suborbital series consists of one bone only which is much higher than broad.

The maxilla is of unusual shape, high posteriorly and with an almost vertical posterior border. The ventral margin bears very small teeth along its entire length, arranged in a single closely set series. Although small, the teeth are of the same shape and arrangement as in *G. punctatus*. The preopercular is a high bone with a gap between it and the opercular. Although it cannot be seen with certainty, a dermohyal element appears to fill this gap. The opercular is almost rectangular, less than one and three-quarter times as high as the subopercular. Below the subopercular are ten branchiostegal rays and a large median gular. A sclerotic ring probably supported the eye.

The lower jaw. Posteriorly the lower jaw is much expanded, giving a high prominence, much as in *Amblypterus* and *Gonatodus.* Anteriorly the jaw is much shallower. The angular bone does not extend very far along the ventral jaw surface and the articular region is ossified. The dentary bears a single series of small closely set teeth. Anteriorly the dentary forms part of the inner jaw surface while the remainder of the inner surface is covered by the prearticular and a coronoid series.

The palate. Although little could be made out, both the ectopterygoid and palatine bear numerous small teeth.

The unpaired fins and their girdles. The supracleithrum extends ventrally beyond the junction of the opercular with the subopercular, the cleithrum is elongate and the clavicle stout. The ornamentation of both supracleithrum and cleithrum is distinct and consists of elongate striae of enamel which follow the long axis of the bone.

The pectoral fin is large with seventeen to nineteen lepidotrichia.

The pelvic fin is smaller with only twelve to thirteen fin rays.

The unpaired fins. Both dorsal and anal fins are triangular with the dorsal fin placed well back. The number of rays cannot be determined with complete accuracy but is not many more than twenty in either fin. The fulcra are distinct, larger than in *Gonatodus.*

The caudal fin is heterocercal, inequilobate and deeply cleft.

All the fin rays are closely articulated and distally bifurcated.

The squamation. The scales are higher than broad on the flank and at the deepest part of the body number around ten to twelve rows. Thus in proportion to body size the scales are large (larger than in *Gonatodus*). The ornamentation can be seen from Text-fig. 6 and consists of two or three striae following the antero-ventral border and of serrations (fine denticulations) posteriorly. The main portion of the scale is smooth apart from numerous punctations.

Scale structure. The scale structure of *Pseudogonatodus parvidens* (Traquair) has already been partly dealt with by Aldinger (1937, fig. 55). In general it resembles that of *Elonichthys.* For a more complete description of the scale structure of *Pseudogonatodus* see under *Pseudogonatodus macrolepis* (Traquair).

LOCALITY AND HORIZON. Carboniferous of Scotland, Namurian to Ammanian (Westphalian A). From the Edge Coal series (Borough Lee Ironstone) at Borough Lee, Loanhead, Wallyford, Possil and Lochgelly. Also from the South Parrot coal seam, Niddrie.

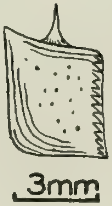

FIG. 6. *Pseudogonatodus parvidens* (Traquair). Anterior flank scale.

Pseudogonatodus macrolepis (Traquair)

(Text-figs. 7–9)

1877 *Gonatodus macrolepis* Traquair : 271.
1877*b* *Gonatodus macrolepis* Traquair : 556.
1881 *Gonatodus macrolepis* Traquair ; Traquair : 35 (name only).
1882 *Gonatodus macrolepis* Traquair ; Traquair : 546.
1890 *Gonatodus macrolepis* Traquair ; Traquair : 391.
1891 *Gonatodus macrolepis* Traquair ; Woodward : 435, pl. 16, fig. 8.
1903 *Gonatodus macrolepis* Traquair ; Traquair : 692, 694, 700, 701.
1907 *Gonatodus macrolepis* Traquair ; Traquair : 97, pl. 20, figs. 9–14, text-fig. 3*b*.
1937 *Gonatodus macrolepis* Traquair ; Aldinger : 212.
1954 *Gonatodus macrolepis* Traquair ; Waterston : 57.

DIAGNOSIS (emended). Fishes not exceeding 18 cm. in total length, body fusiform, length of head contained five times and greatest depth of body little more than four times in total body length. Maxilla of distinctive shape, postero-ventral margin being sharply bent downward, so much so that main blade of maxilla is much higher than broad (see Text-fig. 7). Teeth on jaws large, arranged in single row but of same shape and disposition as in *Pseudogonatodus parvidens* and *Gonatodus punctatus*.

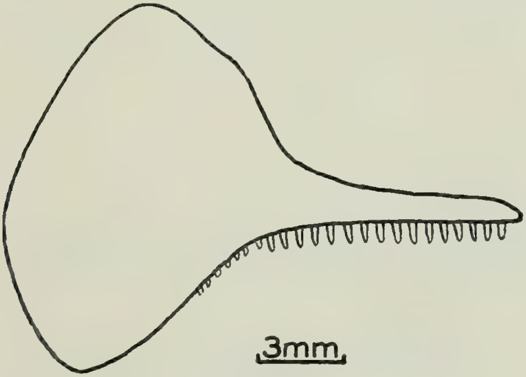

FIG. 7. Maxilla of *Pseudogonatodus macrolepis* (Traquair).

Scales large in proportion to body size, numbering around ten to twelve rows at deepest part of body. Scales deeper than broad on flank, rhomboidal, feebly ornamented with few traces of striae and with finely serrated posterior border. Remainder of scale surface smooth apart from delicate punctures (Text-fig. 8). Again resorption seems to have occurred. Large ridge scales preceding caudal fin.

LECTOTYPE. R.S.M. 1926.57.20 and counterpart B.M.N.H. P.11648, an imperfect fish from the Gilmerton Ironstone, Lower Carboniferous Limestone series, Venturefair Pit, Gilmerton, near Edinburgh. Designated as the " type specimen " by Traquair (1907, pl. 20, fig. 9).

MATERIAL. In addition to the lectotype, six tolerably complete fish, four bodies without heads, three isolated maxillae and one dentary in the British Museum (Natural History) and the Royal Scottish Museum, Edinburgh.

REMARKS. Apart from the shape of the maxilla and the large teeth, this species is very similar to the type species.

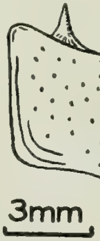

FIG. 8. *Pseudogonatodus macrolepis* (Traquair). Anterior flank scale.

Scale structure. The fine structure of the scale can be seen in Text-fig. 9. In most respects it is similar to that already described in *Gonatodus punctatus* (Agassiz). The arrangement of the canals in both the dentine and the bony lamellae is identical with those in *Gonatodus punctatus*. However, in the scale of *Pseudogonatodus macrolepis* there is a great concentration of fibres of Sharpey which was not observed

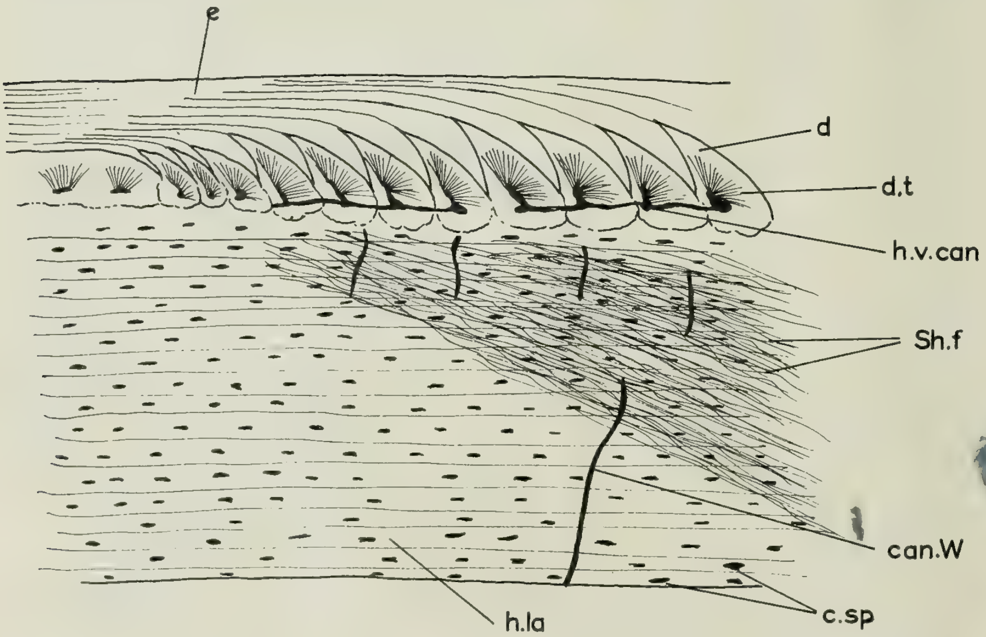

FIG. 9. *Pseudogonatodus macrolepis* (Traquair). Dorso-ventral cross section through mid-lateral scale. ×100. From B.M.N.H. P.11648.

in *Gonatodus punctatus*, while there appears to be a greater number of cell spaces in the bony lamellae of *Pseudogonatodus macrolepis*.

The structure of the scale of *Pseudogonatodus* is close to that of both *Gonatodus* and *Amblypterus*.

LOCALITY AND HORIZON. Lower Carboniferous (Middle to late Visean). A few specimens from the Calciferous Sandstone of Straiton, the remainder from the Gilmerton Ironstone, Venturefair Pit, Gilmerton.

Genus *DRYDENIUS* Traquair 1890

1877*c* *Microconodus* Traquair : 12, 33 (name only, but see also Traquair 1907 : 103).
1888 *Gonatodus* Traquair (*partim*) : 252.

DIAGNOSIS (emended). Body fusiform, dorsal fin placed opposite space between pelvics and anal, both dorsal and anal fins triangular, anal smaller. Caudal fin heterocercal, inequilobate. Pelvics and pectorals with less than ten rays. All fins have small number of rays articulated and distally bifurcated; small fulcra fringe leading edges. Suspensorium appears to have been almost vertical. Teeth on both maxilla and dentary in single series, stout and closely set. Coronoid series also bearing large teeth set in more than one row. Scales very large in proportion to body size, deeper than broad on flank and ornamented with occasional striae.

TYPE SPECIES. *Drydenius insignis* Traquair.

REMARKS. This genus contains but two species. *D. insignis* Traquair and *D. molyneuxi* (Traquair), both of which were placed in it by Traquair (1890 : 392; 1907 : 102). The large scales, stout but few fin rays and the presence of coronoid teeth make the genus readily identifiable. An interesting feature of *Drydenius* is that the maxilla has begun to grow down around the peg-like teeth and partially encases them proximally. In the later genus *Paramblypterus* Sauvage which was derived from the Gonatodidae the maxilla completely encases the teeth apart from the distal tips.

Drydenius insignis Traquair

(Text-figs. 10, 11)

1890 *Drydenius insignis* Traquair : 392, 399.
1891 *Drydenius insignis* Traquair; Woodward : 437.
1903 *Drydenius insignis* Traquair; Traquair : 695, 700, 701.
1907 *Drydenius insignis* Traquair; Traquair : 101, pl. 22, figs. 5–9.
1954 *Drydenius insignis* Traquair; Waterston : 59.

DIAGNOSIS (emended). Fishes not exceeding 13 cm. in total length, body fusiform, dorsal fin opposite space between pelvics and anal. Caudal fin heterocercal and deeply cleft. Length of head contained little more than five times and greatest depth of body four and a half times in total body length. Scales denticulated posteriorly, surface smooth with no ornamentation apart from fine punctations (see Text-fig. 11).

LECTOTYPE. Selected by Waterston (1954 : 59). R.S.M. 1950.38.85, a splenial bone from the Borough Lee Ironstone, Edge Coal Series; Loanhead near Edinburgh.

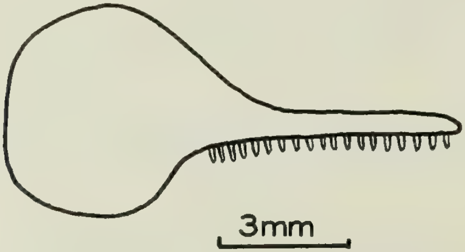

FIG. 10. Maxilla of *Drydenius insignis* Traquair.

MATERIAL. In addition to the Lectotype, two complete fish, one body wanting head, two isolated maxillae, and two splenials in the British Museum (Natural History) and the Royal Scottish Museum.

DESCRIPTION. The external skull bones, including the jaws, are all ornamented with long, relatively stout striae of enamel which more or less follow the length of the bones. The suspensorium appears to be almost upright.

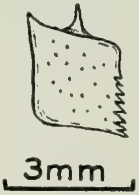

FIG. 11. *Drydenius insignis* Traquair. Anterior flank scale.

On the coronoid series is a single row of very large, stout teeth, and internal to this there are often numerous small granular teeth. The palatal bones also appear to be clothed with small granular teeth. The large teeth on the coronoid are larger than the teeth on the dentary or maxilla.

The maxilla is of unusual shape and quite diagnostic. The main blade is small in comparison with the normal palaeoniscoid maxilla, and not as high as in *Pseudogonatodus macrolepis*. The teeth on the maxilla are large and stout and in a single series along the anterior two-thirds of the bone (Text-fig. 10).

The pectoral fin (R.S.M. 1890.78.18) has from eight to ten lepidotrichia, and is short-based. The pelvic fin has some eight or nine stout rays while the dorsal fin is the largest with from twenty to twenty-two rays. The anal fin has fifteen rays.

The scales are large in proportion to body size, at the deepest part of the body numbering between nine and ten rows. Scales ornamented with striae and punctations; hinder margin denticulated.

LOCALITY AND HORIZON. Carboniferous of Scotland, early Namurian (E_1–E_2). From the Borough Lee Ironstone at Borough Lee and Loanhead. (The Borough Lee Ironstone is a member of the Edge Coal or Middle Carboniferous Limestone series.)

Drydenius molyneuxi (Traquair)

(Text-figs. 12–15)

1877*c* *Microconodus molyneuxi* Traquair : 33 (name only).
1888 *Gonatodus molyneuxi* (Traquair) Traquair : 252.
1890 *Gonatodus molyneuxi* (Traquair) ; Ward : 178, pl. 6, fig. 11.
1891 *Gonatodus molyneuxi* (Traquair) ; Woodward : 436, 437.
1905 *Gonatodus molyneuxi* (Traquair) ; Ward : p. 302, pl. 6, fig. 2.
1907 *Drydenius molyneuxi* (Traquair) Traquair : 102, pl. 20, figs. 6–8.
1919 *Drydenius molyneuxi* (Traquair) ; Pruvost : 425, 426, pl. 29, figs. 6–17.
1930 *Drydenius molyneuxi* (Traquair) ; Pruvost : 130, pl. 1, fig. 5.
1943 *Drydenius molyneuxi* (Traquair) ; Heide : 39, pl. 3, fig. 5*a–f*.
1954 *Drydenius molyneuxi* (Traquair) ; Waterston : 59.
1958 ?*Drydenius* sp. Vangerone : 472, pl. 23, fig. 3.

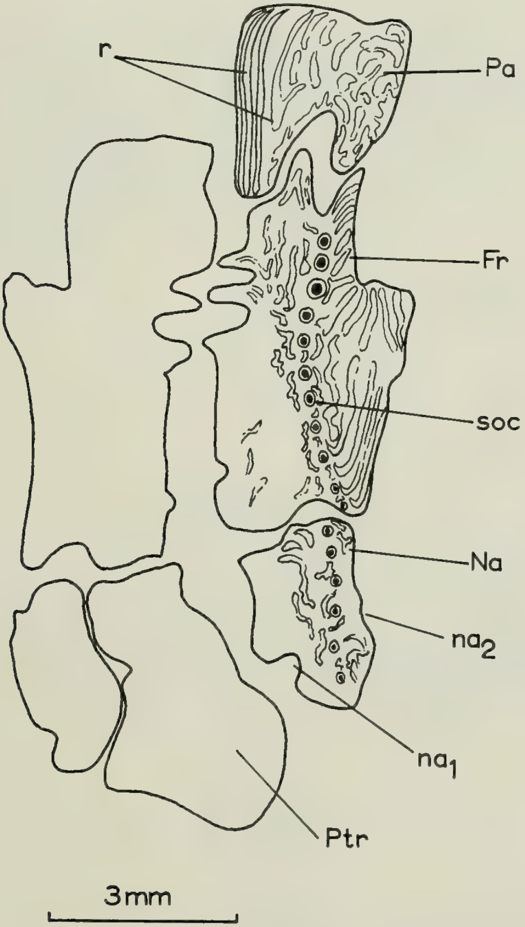

FIG. 12. *Drydenius molyneuxi* (Traquair). Dorsal view of skull roofing bones. From B.M.N.H. P.7973 & counterpart.

DIAGNOSIS (emended). Fishes not exceeding 7 cm. in total length, body fusiform. Length of head contained four a half times, and greatest depth of body a little over four times, in total body length. Blade of maxilla rounded dorsally. Scales very finely denticulated posteriorly (far more denticulations than in *D. insignis*), with fine striations running up diagonally from these denticulations. These fine striae only on posterior third of scale ; anterior portion with few punctures and an occasional stria following anteroventral margin (Text-fig. 14).

LECTOTYPE, here chosen. B.M.N.H. P.7973 and counterpart P.7976, a tolerably complete fish from the Deep Mine Ironstone (Westphalian C), Longton, Staffordshire.

MATERIAL. In addition to the lectotype, five comparatively complete fish, four bodies without skulls, and isolated lower jaws in the British Museum (Natural History) and the Royal Scottish Museum.

DESCRIPTION. The external skull bones including the jaws are ornamented with stout ridges of enamel, which are more or less contorted and not in straight lines as in *D. insignis*, *Pseudogonatodus* and *Gonatodus*. The orbit is large and the snout rounded. The suspensorium is upright and the lower jaw short and stout. The sutures between the frontals and between the frontals and parietals are digitate (Text-fig. 12). The maxilla is of characteristic shape (Text-fig. 13) with a larger blade than in *D. insignis*. The coronoid bears large stout teeth as in *D. insignis*. The second infraorbital is expanded as in *Pseudogonatodus parvidens* and the infraorbital canal much branched posteriorly as it passes through this bone. There are eleven branchiostegal rays and a median gular.

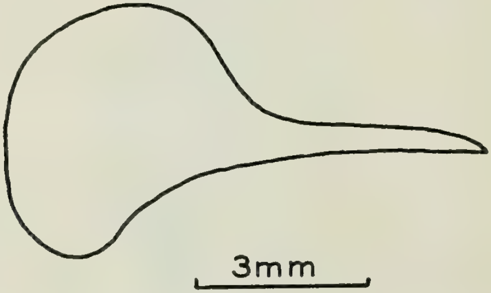

FIG. 13. Maxilla of *Drydenius molyneuxi* (Traquair).

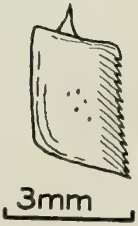

FIG. 14. *Drydenius molyneuxi* (Traquair). Anterior flank scale.

The fins are always poorly preserved. No specimen I have examined shows a pectoral fin, while all that can be said about the anal is that it only possessed a few rays. The pelvics have some seven or eight stout rays and the dorsal about fifteen.

The scales are very large in porportion to body size, at the deepest part of the body numbering between eight and nine rows.

Scale structure. The structure of the scale (Text-fig. 15) is almost identical with that of *Pseudogonatodus macrolepis* (Traquair) even down to the large number of fibres of Sharpey. The bone cells are however larger and considerably fewer in *Drydenius molyneuxi*.

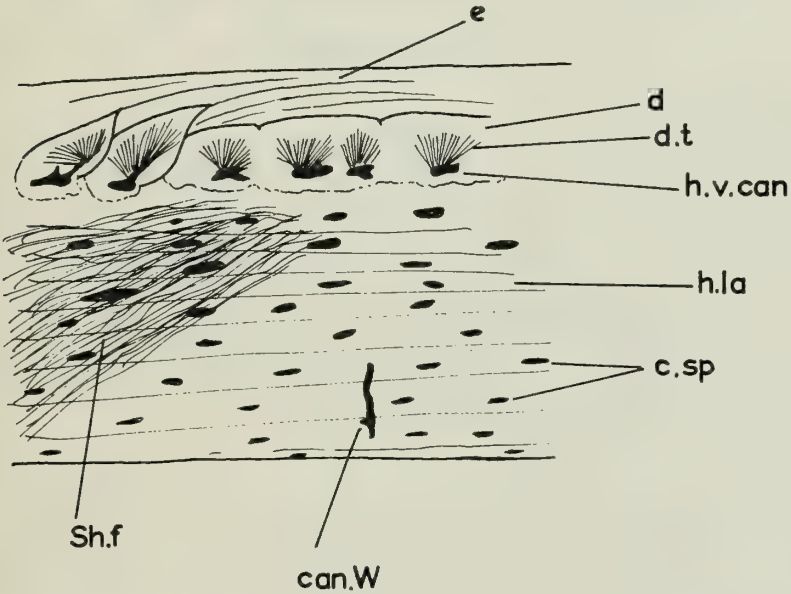

FIG. 15. *Drydenius molyneuxi* (Traquair). Dorso-ventral cross section through mid-lateral scale. ×90. From B.M.N.H. P. 7974.

LOCALITY AND HORIZON. The lectotype came from the North Staffordshire Coal Measures (Westphalian C), in the Deep Mine Ironstone at Longton, Staffordshire. It is also recorded from Broadsfield, Fenton. On the Continent it has been recorded from the Upper Carboniferous of France (Pruvost 1919 : 425), Belgium (Pruvost 1930 : 130 ; Heide 1943 : 39) and, doubtfully, from Aachen, Germany (Vangerone 1958 : 472).

Family **TRISSOLEPIDIDAE** Frič 1893

1936 *Gymnoniscidae* Berg : 345.

DIAGNOSIS. Trunk fusiform ; dorsal fin in front of anal fin. Fin rays of all fins relatively few, articulated but not distally bifurcating. Suprascapular large ; suspensorium upright or nearly so ; snout rounded ; teeth prominent on both jaws and branchiostegal rays numerous. Fins with few stout basal fulcra (Woodward 1942) anteriorly (much as in Phanerorhynchidae) but true series of fulcral scales absent.

REMARKS. Frič (1893) erected the Family Trissolepidae to include *Trissolepis* Frič. Unfortunately *Trissolepis* is a synonym of *Sphaerolepis* Frič. This family contains *Sphaerolepis* Frič and *Sceletophorus* Frič from the Upper Carboniferous. The Trissolepididae were probably derived from the earlier Holuridae and as such show some similarity to the Phanerorhynchidae and to the Teleopterinidae which likewise had their origins in the Holuridae. The Family Atherstoniidae nov. (which includes *Atherstonia* Woodward) are also related to the Trissolepididae.

Genus ***SPHAEROLEPIS*** Frič 1877

1893 *Trissolepis* Frič : 76.

DIAGNOSIS (emended). Trunk fusiform, tail very long ; dorsal fin in front of anal fin, opposite gap between anal and pelvic fins. Dorsal contour arched in advance of dorsal fin ; pectoral fins small, pelvics larger than pectorals. Apart from pelvics all fins have stout basal fulcra (Woodward 1942) forming their leading edges, but true series of fulcral scales absent. All lepidotrichia stout, articulated and not distally bifurcated. Suspensorium upright ; opercular more than three times as deep as subopercular. Dorso-posterior blade of maxilla rounded as in *Pseudogonatodus*. Fossa present in skull roof at junction of parietal, frontal and dermopterotic. Teeth numerous, of moderate size and in one series. Scales cycloidal, those in anterior trunk region being pectinated posteriorly.

TYPE SPECIES. *Sphaerolepis kounoviensis* Frič. The only species.

REMARKS. Frič (1875 : 76) in the first mention of the species *Kounoviensis* merely stated that it belonged to a new genus without erecting a generic name for it. Later in 1877 he placed it in the new genus *Sphaerolepis*. Two years later in his " Fauna der Gaskohle " (1879, **1** : 31) he referred to it as *Sphaerolepis kounoviensis*, but later in the same work (1893, **3**, 2 : 76) changed the name to *Trissolepis kounoviensis* and put it in a new family, the Trissolepidae. Clearly since his original descriptions (1875, 1877) give enough information to recognize the species then the generic name *Sphaerolepis* must stand and *Trissolepis* must be treated as a synonym.

Sphaerolepis kounoviensis Frič

(Plate 1; Text-figs. 16–18)

1875 (Nov. gen.) *Kounoviensis* Frič : 76.
1877 *Sphaerolepis kounoviensis* Frič : 46.
1879 *Sphaerolepis kounoviensis* Frič ; Frič, **1** : 31.
1891 *Sphaerolepis kounoviensis* Frič ; Woodward : 523.
1893 *Trissolepis kounoviensis* (Frič) Frič, **3**, 2 : 76, pls. 109–112, text-figs. 277, 278.
1907 *Sphaerolepis kounoviensis* Frič ; Traquair : 106.
1909 *Sphaerolepis kounoviensis* Frič ; Traquair : 107.
1944 *Trissolepis kounoviensis* (Frič) ; Westoll : 65.

DIAGNOSIS. Fishes not exceeding 11 cm. in total length ; body fusiform, length of head contained almost five times and greatest depth of body just over four times in total body length. Dorsal fin shorter based than anal fin ; two ridge scales in front of dorsal. Fossa present in skull roof at junction of parietal, frontal and dermopterotic.

SYNTYPES. Four specimens in the Národní Museum, Prague, from the Upper Carboniferous of Kounová, Czechoslovakia.

MATERIAL. Photographs and casts of syntypes, and no. 47491 in the British Museum (Natural History).

DESCRIPTION. *The skull.* The bones of the skull and course of the sensory canals are shown in Text-fig. 16. The skull is short and high with an almost vertical suspensorium while the snout is bluntly rounded. The suprascapulars are large, stout and meet in the midline anteriorly. The extrascapular series, consisting of the

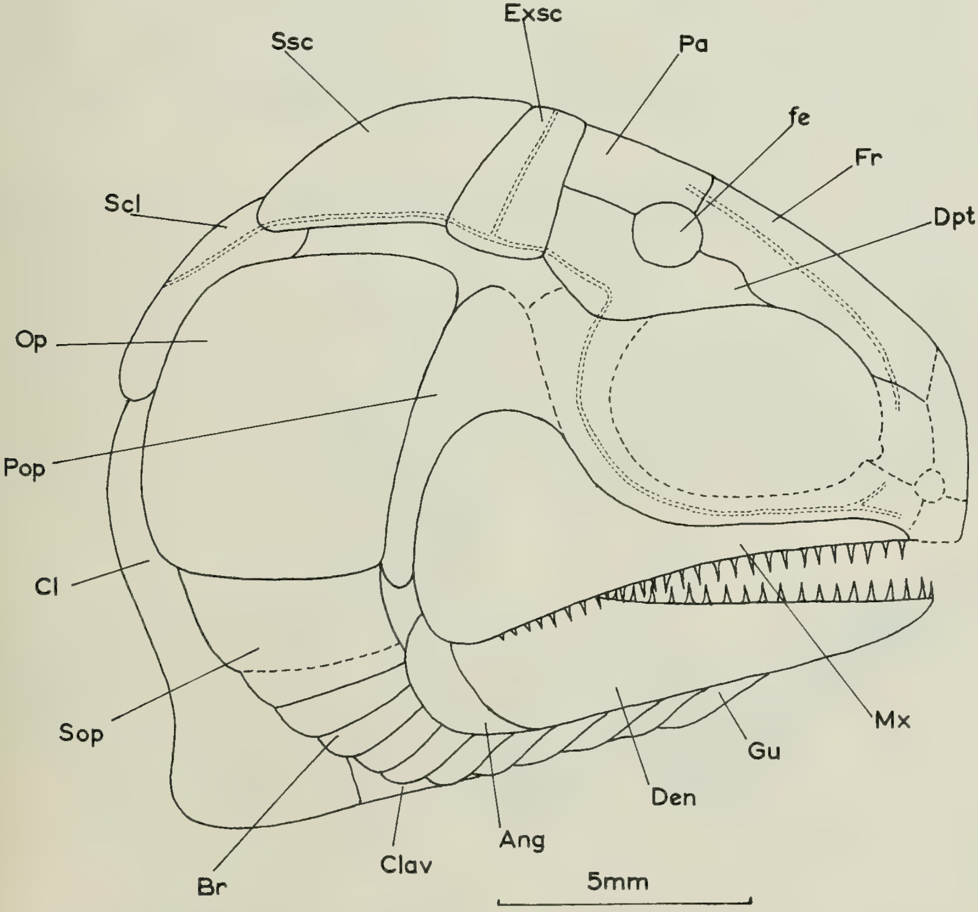

FIG. 16. *Sphaerolepis kounoviensis* Frič. Reconstruction of skull in lateral veiw.

normal single pair of bones, is somewhat larger than in the average palaeoniscoid. The postero-dorsal surface of each extrascapular is peculiarly scalloped. The parietals are almost square while the lateral wall of the skull roof is composed of a short, broad, dermopterotic, but the position and extent of the dermosphenotic is not clear on any of the specimens. Frič (1893, pls. 109–112) in his interpretation of the skull roof indicated a true fossa in the region of the junction between the parietal, frontal and dermopterotic. From a careful study of that region in the specimen concerned I agree with Frič that such a fossa did exist in life and was not caused after death by an otolith as suggested by Westoll (1944 : 65). In this respect *Sphaerolepis* shows some similarity to *Pyritocephalus* Frič (Westoll 1944).

The frontals are large and the nasals and postrostral long, but the remaining bones constituting the snout region could not be distinguished with any degree of certainty although the position of the nares could be seen.

The maxilla is of unusual shape being rounded dorsally as in *Pseudogonatodus* nov. The teeth on the maxilla are of moderate size (somewhat larger than in the normal palaeoniscoid) and arranged in a single series. The preopercular is almost vertical and much narrower than in most palaeoniscoids and in this respect it also resembles *Pseudogonatodus* nov. The opercular is more than three times deeper than broad. Beneath the subopercular are some ten branchiostegal rays with a median gular anteriorly.

Lower jaw. The angular only occupies a small portion of the jaw surface while the dentary is considerably thickened ventrally and forms the major portion of the outer surface of the jaw. A single row of stout teeth is present on the upper margin of the dentary.

The palate. The parasphenoid is short, narrow anteriorly, but expands posteriorly, and in general size and shape is similar to that of *Pteronisculus* White (Nielson 1942). Both the vomers and palatines are large and bear prominent teeth. Those on the palatine are stout, rounded, arranged in a cluster about three deep.

The paired fins and their girdles. The supracleithrum extends about half way down the opercular and the cleithrum is elongated and comparatively stout. A

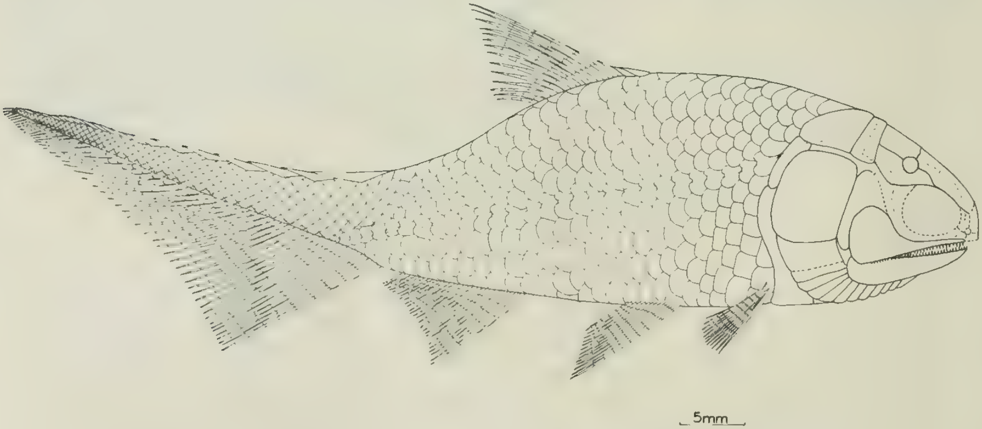

FIG. 17. *Sphaerolepis kounoviensis* Frič. Restoration of whole fish.

distinct ornamentation is visible on both the supracleithrum and the cleithrum, consisting of lines of sharply pointed tubercles that follow the length of the bone. Anteriorly a short clavicle can be seen.

The pectoral fin is small with eleven to thirteen lepidotrichia. Apart from the ray forming the leading edge all the lepidotrichia have distinct articulations.

The pelvic fin is larger with fourteen to sixteen rays, all of them articulated.

The unpaired fins. The dorsal fin is composed of about fifteen stout, articulated lepidotrichia and is preceded by two ridge scales. The anal fin is longer based than the dorsal and is made up of more rays, between twenty-five and twenty-eight. As in the dorsal fin there are two or three basal fulcra (Woodward 1942) in the anal forming a stout leading edge to the fin.

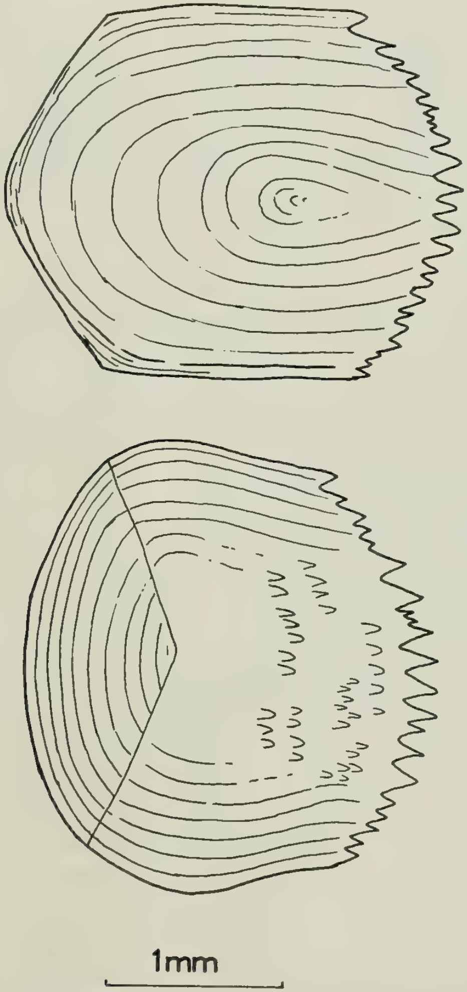

FIG. 18. *Sphaerolepis kounoviensis* Frič. Anterior flank scales.

The caudal fin is heterocercal but not cleft as in most palaeoniscoids, and in this respect *Sphaerolepis* resembles *Phanerorhynchus* Gill, *Palaeoniscinotus* Rohon, *Holurus* Traquair and *Holuropsis* Berg. The rays are all articulated apart from the two stouter ones (basal fulcra) which form the leading edge.

The squamation. The scales, apart from those on the tail, are cycloidal. In this feature *Sphaerolepis* shows some similarity to *Cryphiolepis* Traquair and *Browneichthys* Woodward (Griffith 1958). The exposed surface of the majority of these cycloidal scales is covered with closely-set, fine, concentric ridges of enamel while those in the anterior flank region have a much stronger ornamentation. Thus the first three to four rows of scales behind the pectoral girdle have several rows of backwardly pointing tubercles on the posterior surface and the posterior edge pectinated (Text-fig. 18).

The scales on the caudal body-prolongation are rhombic on the sides and on the dorsal surface form a median row of imbricating, V-shaped scales.

LOCALITY AND HORIZON. All the known specimens came from the " cannel " coal (" gas-coal ") of Kounová, Záboř, Hředl and Kněžoves, which is uppermost Westphalian extending into the lowermost Stephanian (Floral zones H–I).

Genus ***SCELETOPHORUS*** Frič 1894

1894 *Phanerosteon* Traquair ; Frič : 92 (*errore*).
1936 *Gymnoniscus* Berg : 345.

DIAGNOSIS (emended). Trunk fusiform, tail short ; dorsal fin situated in front of anal fin, opposite gap between anal and pelvic fins. Dorsal contour more or less flat ; pectoral and pelvic fins of about same size, both relatively small. All fins with stout basal fulcra (or spines) forming their leading edges, but true series of fulcral scales absent. All fin rays stout, articulated, but not distally bifurcated. Opercular not quite twice as deep as subopercular. Dorso-posterior blade of maxilla rounded as in *Sphaerolepis*. Teeth numerous, of moderate size, arranged in single series. Scales rhomboidal and, for most part, ornamented with fine, concentric ridges of enamel. Ridge scales prominent along dorsal contour.

TYPE SPECIES. *Sceletophorus biserialis* Frič. The only species.

REMARKS. Frič (1894 : 92) also described the new species *Phanerosteon pauper* from the same locality as *Sceletophorus biserialis*. *Phanerosteon pauper* is a small naked form which Frič (1894 : 92) put into Traquair's (1881 : 39) genus *Phanerosteon* even though he thought it possibly the young of *Sceletophorus biserialis*. Later Berg (1936 : 345) erected the new genus *Gymnoniscus* for its reception. Westoll (1944 : 66) believed Frič (1894 : 92) to be right in his suggestion that *Phanerosteon pauper* was probably the young of *Sceletophorus biserialis*, and after a study of the specimen concerned I have no doubt that that is so.

Wade (1935) has already shown in *Brookvalia* that scale development starts behind the pectoral girdle, along the lateral line canal and on the axial lobe of the tail, and this is precisely where scales are to be found on the juvenile form of *Sceletophorus biserialis* Frič. In *Phanerosteon* Traquair and to a certain extent in *Carboveles* White (1927) the development of scales has been arrested at this point and thus they both provide examples of paedomorphosis.

Sceletophorus biserialis Frič

(Plates 2, 3 ; Text-figs. 19–21)

1894 *Sceletophorus biserialis* Frič, **3**, 3 : 88, pls. 116, 117.
1894 *Phanerosteon pauper* Frič, **3**, 3 : 92, pl. 117.
1912 *Phanerosteon pauper* Frič ; Traquair : 168.
1936 *Gymnoniscus pauper* (Frič) Berg : 345.
1944 *Sceletophorus biserialis* Frič ; Westoll : 65.
1944 *Phanerosteon pauper* Frič ; Westoll : 66.

DIAGNOSIS. Fishes not exceeding 6 cm. in total length, body fusiform, length of head contained just over four times and greatest depth of body just under four times

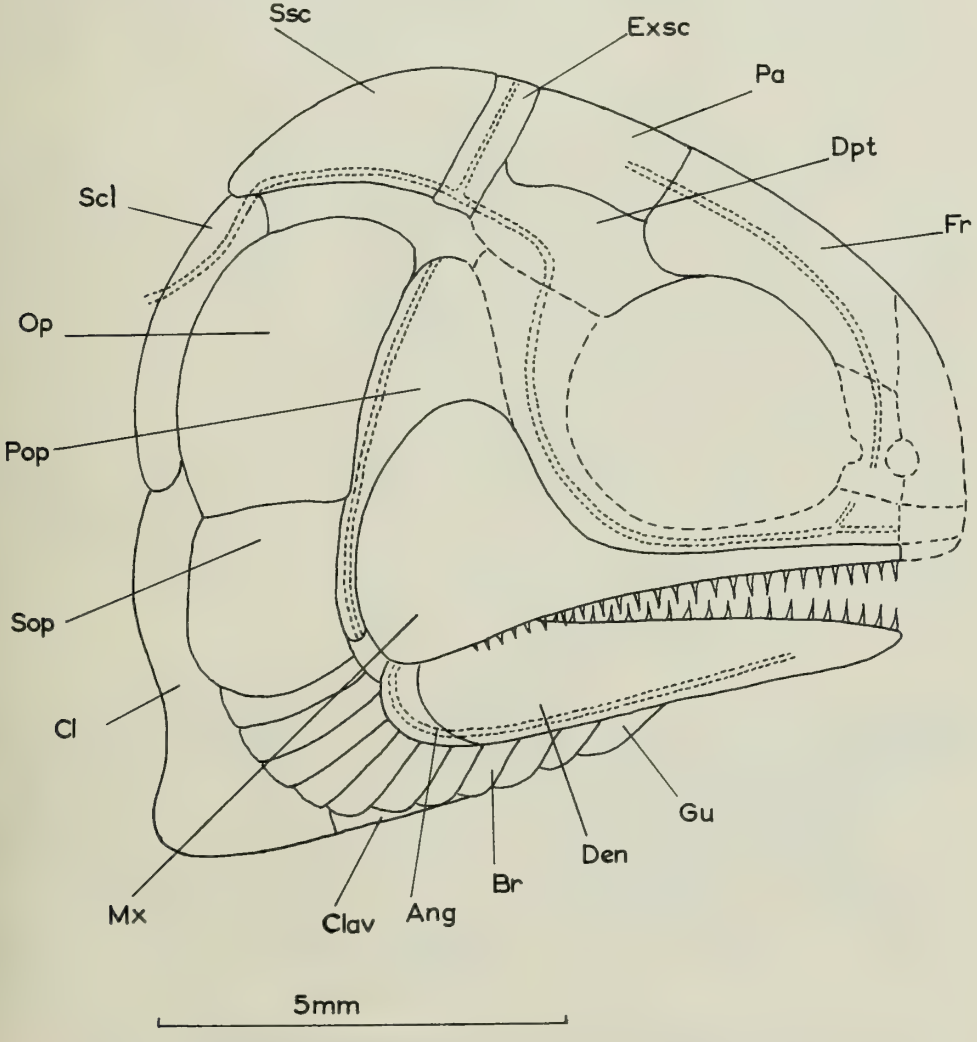

FIG. 19. *Sceletophorus biserialis* Frič. Reconstruction of skull in lateral view.

in total body length. Four ridge scales in front of dorsal fin with paired basal fulcra. Series of large ridge scales running from immediately behind dorsal fin to tip of tail. Single ridge scale in front of anal fin.

SYNTYPES. Both the two syntypes of *Scletophorus biserialis* Frič and the two syntypes of *Phanerosteon pauper* Frič are in the Národní Museum, Prague. All are from the Upper Carboniferous of Třemošná, Czechoslovakia.

MATERIAL. Photographs and casts of syntypes.

DESCRIPTION. *The skull.* The skull is large in comparison to total body length. The suspensorium is vertical and the snout bluntly rounded. The suprascapulars are large and the extrascapulars narrow. In front of the extrascapulars are a pair of large, rectangular parietals which are followed by equally stout frontals. The post-rostral and nasals are long and narrow, but the bones making up the lateral roof of the skull could not be distinguished with any degree of accuracy. However there is no evidence of a fossa in the skull roof as in *Sphaerolepis* Frič.

The maxilla is rounded postero-dorsally much as in *Sphaerolepis* and *Pseudogonatodus*. The teeth on the maxilla are of moderate size, arranged in a single row and similar to those in *Sphaerolepis*. The preopercular is nearly vertical and shaped much as in *Sphaerolepis*. However the opercular is less than twice as deep as the subopercular and considerably deeper than it is broad. Beneath the subopercular are about ten branchiostegal rays with a median gular anteriorly.

The lower jaw. Again very similar to *Sphaerolepis* with the angular only occupying a small portion of the jaw surface and the dentary thickened ventrally. A single row of stout teeth is borne on the upper margin of the dentary.

The axial skeleton. The neural and haemal arches are seen as distinct ossifications (see Pl. 2). The ossified vertebral centra (Wirbelröhre) figured by Frič in *Scletophorus biserialis* (1894, fig. 286) and also in *Phanerosteon pauper* (1894, fig. 287) do not exist: what Frič saw was the lateral line canal of the opposite side of the body, which shows through the body scaling as a segmental, tubular structure, in such a position (due to post mortem twisting of the body) as to be aligned in the gap between the anterior neural and haemal arches (Pl. 2).

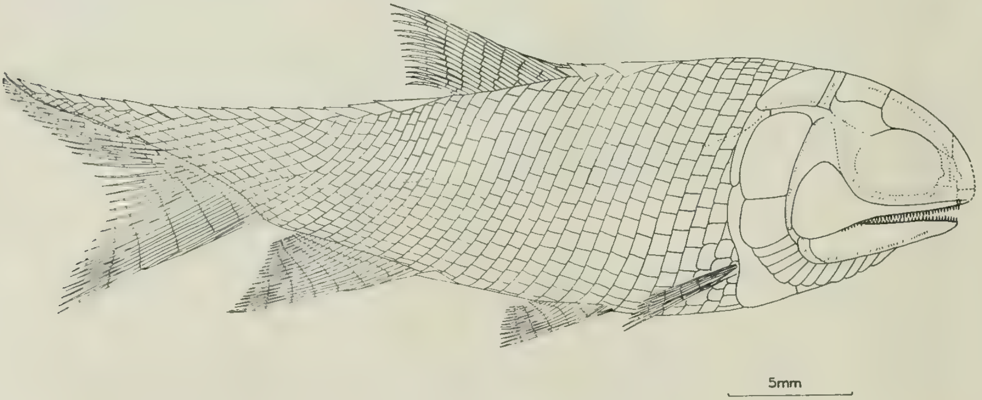

FIG. 20. *Sceletophorus biserialis* Frič. Restoration of whole fish.

The paired fins and their girdles. The supracleithrum is longer than in *Sphaerolepis* and extends over two-thirds of the way down the opercular. The cleithrum is broad and anteriorly united with a short clavicle.

The pectoral fin is longer than the pelvic and composed of only eight rays. Anteriorly the leading edge is made up of three, short, stout unarticulated basal fulcra (Woodward 1942). Frič (1894, pls. 116, 117) in his reconstruction of *Sceletophorus biserialis* figures some sixteen lepidotrichia in the pectoral fin, but again he was misled by the impression of the pectoral fin of the opposite side which shows through the body scaling (Pl. 2).

The pelvic fin contains about thirteen lepidotrichia all of which are stout and articulated. At the leading edge of the fin there are three short, unarticulated basal fulcra.

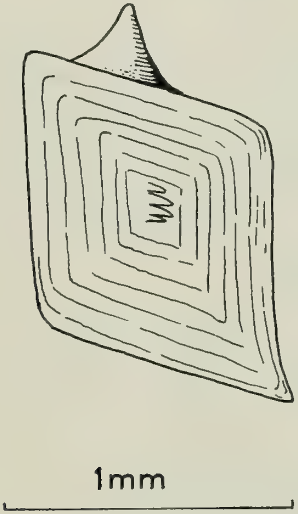

FIG. 21. *Sceletophorus biserialis* Frič. Anterior flank scale.

The unpaired fins. The dorsal fin has between fifteen and seventeen articulated fin rays with the leading edge reinforced by three pairs of unarticulated basal fulcra.

The anal fin is longer with some twenty robust articulated rays. The leading edge is again strengthened by three unarticulated basal fulcra which unlike those in front of the dorsal fin are unpaired.

The caudal fin is heterocercal and only partially cleft, shorter than in *Sphaerolepis*. The rays are stout and articulated and again there are three or four strong, unarticulated basal fulcra preceding it.

The squamation. The scales are rhomboidal and ornamented with fine concentric ridges of enamel, but the scales immediately around the pectoral fin are almost cycloidal while those in the anterior flank region have in addition to the fine concentric ridges of enamel two or three small backwardly directed spines in the mid-scale region.

Locality and horizon. All the known specimens came from the " cannel " coal of Třemošná, which is uppermost Westphalian extending into the lowermost Stephanian (Floral zones H–I).

Family **PHANERORHYNCHIDAE** Stensiö 1932

Diagnosis. As for the genus *Phanerorhynchus*.

Remarks. This family includes the single genus *Phanerorhynchus* Gill. The peculiar nature of its fins suggests a relationship to the Haplolepiformes while the skull could easily have been derived from that of a primitive haplolepid-like form by elongation of the snout region. Like the Haplolepiformes the Phanerorhynchidae were probably derived from the earlier Holuridae. Superficially the Phanerorhynchidae show considerable similarity to the later Chondrosteiformes and Acipenseriformes.

Genus ***PHANERORHYNCHUS*** Gill 1923

Diagnosis. Body fusiform ; dorsal fin almost opposite anal fin, both fins triangular, anal smaller of two, form of caudal fin unknown. Pectoral and pelvic fins small ; all fins with stout, unjointed rays which never bifurcate. Snout drawn out as distinct rostrum projecting well beyond anterior limit of lower jaw. Suspensorium almost vertical, opercular more ovoid than rectangular. Orbit small, dentition feeble or absent. Scales large, dorsal and ventral ridge scales prominent, ridge scales graduating into very stout basal fulcra (Woodward 1942) in front of fins (true fulcral scales absent).

Type species. *Phanerorhynchus armatus* Gill, the only known member of the genus.

Phanerorhynchus armatus Gill

(Text-figs. 22,23)

1915 Imperfectly preserved small fish, Woodward : 73.
1923 *Phanerorhynchus armatus* Gill : 465, text-fig. 1.
1932 *Phanerorhynchus armatus* Gill ; Stensiö : 78, text-fig. 29.
1936 *Phanerorhynchus* Gill ; Berg : 345.
1939 *Phanerorhynchus armatus* Gill ; Moy-Thomas : 118, text-fig. 31*a*.

Diagnosis. Fishes not exceeding 4 cm. in total length, body fusiform, length of head contained slightly more than three times and greatest depth of body three times in total body length. Lepidotrichia stout, smooth, unjointed and not bifurcated. Scales large, median flank row containing lateral line about three times deeper than broad. Only six obvious scale rows. Dorsal ridge scales with stout spines graduating into basal fulcra in front of dorsal fin. Ventral ridge scales prominent but with less obvious spines.

Holotype. Manchester Museum, L.8585, an almost complete specimen, minus tail, in a clay ironstone nodule ; the only known specimen of this species. From the Middle Coal Measures of Sparth, Lancashire.

Description. *The skull.* The general shape of the skull can be seen from Text-fig. 22. The anterior end is drawn out into a very distinct rostrum. The suprascapulars are large and are joined to a pair of extrascapulars anteriorly. The parietals

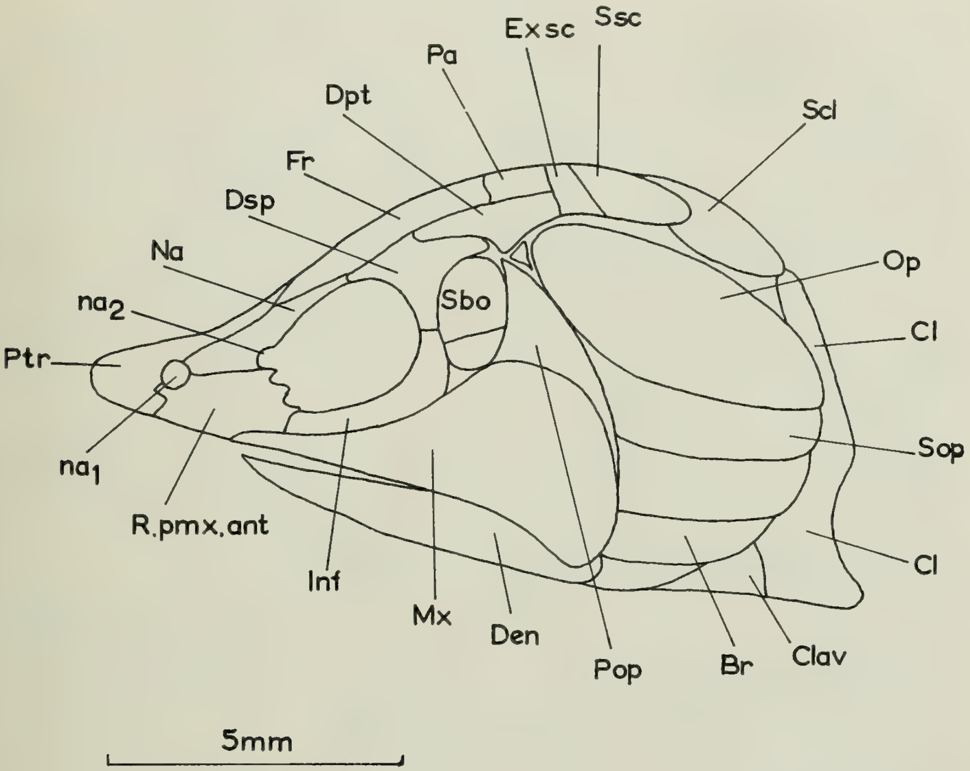

FIG. 22. *Phanerorhynchus armatus* Gill. Reconstruction of skull in lateral view.

are relatively small and square in outline, while the frontals are long with their anterior margins produced into a point thus giving the postrostral a V-shaped insertion between the two frontals. On either side of the single median postrostral is a stout, long, nasal element. The nasal is broad and its lateral margin has an emargination (*na*₂) which indicates the position of the posterior nostril. The anterior nostril (*na*₁) lies between the nasal, postrostral and rostro-premaxillo-antorbital. Posteriorly the nasal joins the frontal and the dermosphenotic, anteriorly the rostro-premaxillo-antorbital. The postrostral is only slightly convex transversely in its posterior half, but the anterior half of the bone is strongly curved in a transverse as well as longitudinal direction, giving the head a distinct rostrum. Ventrally the postrostral meets the paired rostro-premaxillo-antorbitals. The rostro-premaxillo-antorbital is notched anterio-dorsally (*na*₂) while posteriorly it is ornamented with several backwardly pointing short spines. Dorsally it articulates with the nasal and posteriorly with both the maxilla and infraorbital.

The lateral wall of the skull roof comprises two bones, the dermopterotic and the dermosphenotic. The dermopterotic is broad posteriorly but tapers almost to a point anteriorly where it fits between the dermosphenotic and the frontal. The dermosphenotic is larger than the dermopterotic and anteriorly meets the nasal. Ventrally the dermosphenotic abuts against the apparently single, long, curved infraorbital bone. Behind the infraorbital and below and behind the dermosphenotic are two suborbitals, of which the dorsal is by far the larger.

The maxilla is of the normal palaeoniscoid outline, but its anterior prolongation is somewhat short ; it is ornamented with concentric striae of enamel. The preopercular is again of the normal palaeoniscoid form and from the inclination of its posterior border the suspensorium can be seen to be almost upright. The opercular is large, ovoid in shape and ornamented with sparse longitudinal ridges of enamel. The subopercular is much smaller and scarcely larger than the succeeding branchiostegal ray. At least four branchiostegal rays can be seen, but whether or not a gular plate is present could not be determined. As already mentioned by Watson (*in* Gill 1923) there appears to be a small triangular plate between the top of the preopercular and the dermopterotic.

The lower jaw. The lower jaw is ornamented with longitudinal striae of enamel, but apart from the mandibular sensory canal with its three lateral tubules running out obliquely towards the surface of the jaw little could be made out. Whether or not teeth were present could not be determined : if present they must have been very small.

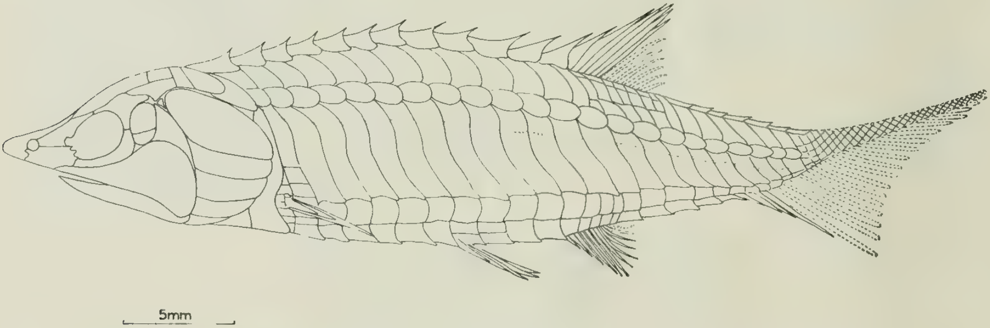

FIG. 23. *Phanerorhynchus armatus* Gill. Restoration of whole fish.

The paired fins and their girdles. Of the pectoral girdle, the supracleithrum and cleithrum are ornamented with concentric ridges of enamel which run parallel to the margins, nearer the centre of the bones these ridges give way to tubercles. The supracleithrum and cleithrum are of normal palaeoniscoid proportions and ventrally there is a pair of stout clavicles. Of the pectoral fin, only the base and one fulcral scale are to be seen on the specimen, but probably there were four to eight fin rays. The pelvic fin has a very short base and is composed of four to six rays.

The unpaired fins. Both the dorsal and anal fins are small, situated far back and almost opposite one another, the dorsal being slightly the larger. Of the dorsal fin, some six rays can be seen with certainty but the total number was probably nearer twelve. On the anal fin about nine rays can be counted, but again there may have been one or two more. Only the base of the slender tail shaft is preserved, with two very stout fulcra ventrally, followed by three stout fin rays.

The squamation. The body scales have been somewhat distorted but the true arrangement is given in Text-fig. 23. On each of the largest, middle flank scales there are two distinct tubercles, one near the dorsal edge and the other two-thirds of the way down : the dorsal one represents the passage of the lateral line. The first row of scales beneath the dorsal ridge scales also has a large tubercle near the base of each scale. All these tubercles are long and point posteriorly, often extending beyond the posterior margin of the scale in which they arise.

The dorsal row of ridge scales is composed of single scales, but the ventral row consists of paired scales up to the pelvic fin. After the anal fin the ridge scales are single and unpaired.

LOCALITY AND HORIZON. Sparth, near Rochdale, Lancashire. Middle Coal Measures, Upper Carboniferous, Ammanian (*Anthracoceras* Zone A).

Family **OSORIOICHTHYIDAE** nov.

DIAGNOSIS. Trunk fusiform ; mandibular suspension moderately oblique, pectoral fins with large number of articulated and distally bifurcating rays. Rostrum well developed, teeth arranged in single series. Opercular small, with accessory opercular separating it completely from subopercular, all three bones approximately same size. Branchiostegal rays very numerous, gular large ; scales small and rhomboidal.

REMARKS. This family has been erected to include the single genus *Osorioichthys* Casier from the Upper Devonian of Belgium. The condition of the opercular apparatus separates it from all other described genera with the exception of *Rhabdolepis* Troschel (Gardiner 1963). It differs from *Rhabdolepis* in the more primitive arrangement of the skull roof and in the large size of the accessory opercular in relation to the opercular. The Osorioichthyidae represents a specialized side line from the main palaeoniscoid stock.

Family **GYROLEPIDOTIDAE** nov.

DIAGNOSIS. Body fusiform ; dorsal fin arising just anterior to anal fin ; both fins of moderate size ; caudal fin powerful, deeply cleft, equilobate. Paired fins moderate to large. All fins with large, articulated and distally bifurcating rays, and stout fulcra anteriorly. Skull rounded anteriorly without well developed rostrum ; suspensorium only slightly inclined, opercular high and subopercular somewhat reduced ; dermohyal large, but no accessory opercular present. Dermopterotic long, suborbital series well defined, teeth stout and in single series. Large dorsal ridge scales running from occiput to dorsal fin and from dorsal fin to caudal extremity ; large ventral scales extending from anal fin to base of caudal.

REMARKS. This family includes *Gyrolepidotus* Rohon and *Palaeobergia* Matveeva from the Lower Carboniferous of Russia. It belongs to a closely related complex of families including the Carbovelidae, Gonatodidae *nov*, Cosmoptychiidae, Acrolepididae, Elonichthyidae, Rhadinichthyidae, Canobiidae, Pygopteridae, Rhabdolepididae, Styracopteridae and Cryphiolepididae. All possess many features in common and were derived from the same stock. The Gyrolepidotidae however can be separated from any one of these families by the stout nature of the fin rays, the very large fulcral scales and the large size of the dermohyal.

Family **AMPHICENTRIDAE** Moy-Thomas 1939 : 115

DIAGNOSIS (emended). Body very deeply fusiform ; dorsal and anal fins triangular and long based, caudal fin heterocercal, inequilobate and deeply cleft : lepidotrichia of all fins jointed and distally bifurcated ; fulcral scales large. Suspensorium almost vertical, orbit small, opercular smaller than subopercular, maxilla triangular and massive. Gular narrow, flank scales deeper than broad ; dentition modified for crushing. Ectopterygoids and coronoids with robust teeth.

REMARKS. This family includes the following genera : *Chirodus* M'Coy, *Cheirodopsis* Traquair, *Eurynothus* Agassiz, *Eurynotoides* Berg, *Paraeurynotus* Chabakov, *Globulodus* Munster, *Protoeurynotus* Moy-Thomas & Dyne and possibly *Tompaichthys* Obruchev. Moy-Thomas (1939 : 115) first recognized that the platysomids could be separated into two distinct families and within the Amphicentridae he included *Amphicentrum* Young, *Protoeurynotus* Moy-Thomas & Dyne, *Eurynotus* Agassiz and *Cheirodopsis* Traquair. However *Amphicentrum* Young 1866 is synonymous with *Chirodus* M'Coy 1848 (Dyne 1939 : 195).

Family **ATHERSTONIIDAE** nov.

DIAGNOSIS. Body fusiform ; dorsal fin arises well in front of anal fin ; both fins triangular. Pectoral and pelvic fins large, anterior rays of pectoral unarticulated proximally. All fins with numerous small fulcra anteriorly and rays closely articulated but *not* distally bifurcated. Skull with moderately developed rostrum and oblique suspensorium. Opercular much larger than subopercular. Scales rhomboidal with pronounced ridges of enamel ; large ridge scales running from occiput to dorsal fin.

REMARKS. The family includes the single genus *Atherstonia* Woodward which ranges from the Upper Permian to the Upper Triassic. The Atherstoniidae are close to the Trissolepididae, particularly in the make-up of the fins in which the rays are not bifurcated distally. They differ from the Trissolepididae in the presence of fulcral scales, in the absence of basal fulcra and in the more oblique suspensorium.

Family **LAWNIIDAE** nov.

DIAGNOSIS. Body fusiform ; dorsal fin large, arising anterior to smaller anal fin ; caudal fin powerful, deeply cleft and inequilobate. Paired fins stout, of moderate size. Lepidotrichia of all fins closely articulated and distally bifurcated ; small fulcral scales present along leading edges of fins. Skull without well-developed rostrum, suspensorium only moderately oblique, opercular and subopercular of approximately same size. Preopercular high, with small dermohyal between it and opercular. Posterior nasal aperture (nostril) completely enclosed posteriorly by antorbital (a specialization not normally seen below holostean grade). Teeth stout and in single series. Ridge scales present in front of unpaired fins.

Remarks. The Family Lawniidae is used to include a single fresh water genus *Lawnia* Wilson (1953), from the Permian of Texas. In body shape, disposition of fins and scale structure this family resembles both the Amblypteridae and the earlier Gonatodidae, but the specialized arrangement of the snout in the Lawniidae clearly separates it from either of these families.

Family **COSMOLEPIDIDAE** nov.

Diagnosis. Trunk elegantly fusiform ; dorsal and anal fins triangular, with posterior rays very short. Dorsal fin opposed to space between pelvics and anal, caudal fin deeply forked, inequilobate and with upper lobe much attenuated. All fins of moderate or small size with broad, articulated rays, distally bifurcating. Rays of pectoral fins unarticulated proximally, minute fulcra on all fins. Mandibular suspensorium oblique, teeth consisting of inner series of stout conical laniaries and outer series of more numerous smaller teeth. Supraorbital sensory canal unites with infraorbital canal. Scales thick and small.

Remarks. The Cosmolepididae is another monogeneric family, containing the Lower Liassic *Cosmolepis* Egerton. This family resembles the earlier Palaeoniscidae in general body form, but can be distinguished from it by the greater length of the jaws, the more oblique suspensorium and the structure of the scales. A diagnostic character is that the supraorbital sensory canal unites with the infraorbital canal, a condition seen in only one other chondrostean (*Brookvalia* Wade).

Family **BRACHYDEGMIDAE** nov.

Diagnosis. Skull without pronounced rostrum, suspensorium almost upright, orbit small ; opercular and preopercular of comparable size, preopercular high and with several dermohyals between it and opercular series. Branchiostegal rays numerous and suborbital series present. Maxilla stout, with very large teeth on anterior half. Large teeth in single series on dentary and rostro-premaxillary. Form of body and fins unknown.

Remarks. This family is used to include the single genus *Brachydegma* Dunkle (1939), from the Texas Permian. The skull is stout and quite unlike that of any other known palaeoniscoid. On the evidence of scale structure and the shape of the preopercular the Brachydegmidae appear to be nearer the Amblypteridae than any other described family.

Family **BOREOSOMIDAE** nov.

Diagnosis. Body fusiform ; dorsal fin arises in advance of pelvics ; anal fin small, remote ; caudal fin heterocercal, moderately to deeply cleft. Lepidotrichia of fins articulated, distally bifurcated ; fulcra present on all fins. Skull with pronounced rostrum, almost upright suspensorium, high preopercular, and both dermohyals and suborbitals present.

Remarks. The family is erected to include the wide-ranging genus *Boreosomus* Stensiö, while *Mesembroniscus* Wade from the Trias of Australia also possibly belongs here. The Boreosomidae show some affinities to the Palaeoniscidae but are distinguishable from the Palaeoniscidae by the more vertical suspensorium, the high preopercular, the shape of the maxilla, the shorter jaws and the anterior postion of the dorsal fin.

Order PELTOPLEURIFORMES

Family **HABROICHTHYIDAE** nov.

Diagnosis. Body fusiform ; dorsal fin arising in front of anal fin, both fins small and triangular. Caudal fin strongly forked and superficially homocercal ; paired fins small. All fins comprise few, stout rays bifurcated distally and (except in caudal) unjointed proximally ; fulcral scales absent. Skull large, suspensorium upright, opercular at least twice as high as subopercular ; maxilla palaeoniscoid in shape, preopercular large, with vertical posterior margin. Dentition feeble, scaling reduced to single row of greatly deepened scales on flank. Posteriorly this scaling terminates in enlarged, symmetrical, semicircular scale.

Remarks. This family is erected to include the single genus *Habroichthys* Brough, which is readily distinguished from the Peltopleuridae by the presence of the single row of greatly deepened scales on the flank.

III. DISCUSSION

Subclass *CHONDROSTEI*

Although the first undoubted members of the class Actinopterygii are found in the Middle Devonian, it seems probable that certain isolated scales recorded from the Lower Devonian (personal observation) may belong to this class. Comparatively rare at first, the actinopterygians flourished, until today they are the most numerous of the vertebrates. The actinopterygians, like the crossopterygians and dipnoans, probably had their origin in salt water (White 1958). However, by the Upper Devonian the actinopterygians were to be found in both freshwater and marine environments and it seems likely that the primitive actinopterygians were tolerant to both salt and freshwater conditions. Only by this assumption can the world-wide distribution of the palaeoniscoids in the Upper Devonian and Lower Carboniferous be explained. By the beginning of the Mesozoic Era the actinopterygians were almost entirely marine and this has been the main centre of their evolution ever since. Today the vast majority of teleosts are marine and of the freshwater forms many have returned secondarily to this environment from salt water (Romer 1945).

For the sake of convenience, the actinopterygians are divided into four groups which are given Subclass status, in ascending order : the Chondrostei, the Holostei, the Halecostomi and the Teleostei. These groups represent grades of evolutionary development rather than natural subdivisions. During the Palaeozoic the evolution of the Actinopterygii consisted of modifications of the original basic chondrostean design and resulted mainly in abortive attempts to reach the holostean level of organization. In the past it has been customary to group all these [abortive] attempts, together with the more successful ones, into the Subclass (or order) " Subholostei " (Brough 1936, 1939), but this has been abandoned since it not only cuts completely across phyletic lines but was based on adaptive characters. The same criticism can be levelled at the Holostei (which include two distinct lineages) but this group, although not a monophyletic one, includes members which at least have all attained the same grade of structural organization.

The Subclass Chondrostei contains all the Palaeozoic actinopterygians (with one late Permian exception) and although still well represented in the early Mesozoic, its members dwindled rapidly in the late Triassic (as they were replaced by the better adapted holosteans to which they had given rise) until today there are some eight degenerate survivors (*Acipenser* Linnaeus, *Huso* Brandt, *Scaphirhynchus* Heckel, *Kessleria* Bogdanon, *Polyodon* Schneider, *Psephurus* Guenther, *Erpetoichthys* Smith and *Polypterus* Lacépède.) from two orders (Acipenseriformes, Polypteriformes).

The Holostei are the characteristic actinopterygians of the Mesozoic ; the earliest member is recorded from the late Permian (Gill 1923*a*) while today there are but two survivors from two distinct orders, the Semionotiformes (*Lepisosteus*) and the Amiiformes (*Amia*).

The Halecostomi enter the fossil record in the early Mesozoic (Rayner 1937 ; Gardiner 1960) and evolved contemporaneously with the Holostei : they disappeared at the end of the Mesozoic, having given rise to the teleosts.

The Teleostei appeared in the Upper Jurassic : the majority of the present day orders can be distinguished in the Upper Cretaceous, while the majority of modern families seem to have arisen in the Eocene or later.

The early actinopterygians are separated from the crossopterygians and dipnoans by their possession of so-called " ganoid scales ". However, these have undergone considerable modification and reduction in the later members, leaving a relatively thin, simple scale. The " ganoid scale " consists of the same three basic units as in the " cosmoid scale ", a basal portion of bone arranged in parallel layers and an upper portion of dentine (cosmine) capped with layers of enamel (ganoine) : separating the two is a spongy layer representing blood vessel plexuses. The central unit of the " ganoid scale " is equivalent to the basic unit of the " cosmoid scale " and the remainder of the scale arises by the deposition in onion-like fashion of concentric layers of all three materials (bone, dentine and enamel) around this central unit. In the light of the " lepidomorial theory " (Jarvik 1960 ; Stensiö 1961) it would appear that the " ganoid scale " is more complex than the " cosmoid " in that units, instead of being added to the edges, arise in complete rings. In other words, the primordia which go to make up the scale have reached a much higher level of fusion in the " ganoid scale ".

In most Mesozoic forms the scales lose the middle dentine layer and the enamel covering becomes thin in many holosteans and halecostomes, disappearing completely in the teleosts, while in some cases the entire scaly covering may be reduced or lost (pycnodonts and some teleosts). Most of these changes are possibly linked with a need of greater flexibility for more efficient swimming.

The " ganoid scale " of the early actinopterygian *Cheirolepis* is very close in structure to the scales of acanthodians (Gross 1947) and it would seem that the actinopterygians and acanthodians were derived from the same ancestral stock.

The actinopterygians, by virtue of several evolutionary bursts, are a large and diverse group and it is not easy to give a comprehensive definition of such a varied assemblage. However they differ from the majority of crossopterygians and dipnoans (with the exception of the coelacanths) in the absence of internal nostrils. Both nostrils are borne high on the face in primitive forms and the two nares of either side are always separated by the supraorbital sensory canal, although in subsequent evolution the two nostrils become confluent (Gardiner 1963). They differ further from the crossopterygians and dipnoans in the arrangement of the sensory canals of the head, the preopercular canal rarely if ever uniting with the postorbital portion of the infraorbital canal as it does in all crossopterygians. Other points of contrast are to be seen in the nature of the paired and unpaired fins. In the actinopterygians the internal skeleton of the unpaired fins is never concentrated into basal plates but normally consists of separate radials. The paired fins primarily do not have the large fleshy lobes seen in the crossopterygians and dipnoans, but instead the entire fin web is supported by long-based, flexible lepidotrichia which do not have the radials concentrated at their bases. In the more advanced teleosts these fins become much narrower at the point of insertion and consequently much more flexible in their movements. There is normally a single dorsal fin in contrast to the two seen in crossopterygians.

The arrangement of the dermal bones of the head in the early actinopterygians is very similar to that seen in the crossopterygians.

Order PALAEONISCIFORMES

The earliest actinopterygians belong to the Order Palaeonisciformes. This order had its beginnings in the Lower Devonian and the first undoubted members are recorded from Middle Devonian freshwater and marine deposits (Guppy, Lindner, Rattigan & Casey 1958). The Palaeonisciformes attained their maximum development during the Carboniferous and Permian when they were the commonest freshwater fishes, while many had also invaded the seas. They were world-wide in distribution during the Palaeozoic Era, being recorded from Great Britain, many parts of Europe, Greenland, Antarctica, Northern Asia, South and East Africa, South and North America and Australia. Of the thirty-nine families so far recognized, twelve survived into the early Mesozoic, but by the Lower Jurassic only three families remained. However, these three families retained the basic palaeoniscoid condition practically unaltered to the last. One of these three is the Family Coccolepididae, containing the single genus *Coccolepis*, which ranges upwards from the Lower Lias (*Coccolepis liassica*) to the Wealden (*Coccolepis macroptera*) and includes the last members of the Palaeonisciformes. The Palaeonisciformes as a group declined rapidly at the close of the Permian, and by the Middle Triassic they had ceased to be a major constituent of the fish fauna. This very rapid decline can be correlated with the advent of more highly evolved groups of chondrosteans (Perleidiformes, Saurichthyiformes, Pholidopleuriformes, etc.) in the early Triassic.

The Palaeonisciformes represent the basal stock of the actinopterygians and from them all the other actinopterygians evolved.

Basically the palaeoniscoids form a closely-knit group, with most of the members very similar in make up. Owing to inaccurate descriptions it has not hitherto been possible to group the palaeoniscoids effectively in families. However, in the light of more recent researches one may at least attempt to group most of the genera with some assurance. Thus the Devonian palaeoniscoids fall into four distinct families—the Cheirolepididae (*Cheirolepis*), the Stegotrachelidae (*Stegotrachelus, Moythomasia,* etc.), the Tegeolepididae (*Tegeolepis*) and the Osorioichthyidae *nov.* (*Osorioichthys*). However, although all these families are fairly generalized, none of them gave rise to any of the other palaeoniscoid families. The most typical palaeoniscoids belong to the families Elonichthyidae, Acrolepididae, Palaeoniscidae and Coccolepididae, and these families belong to the central stem of palaeoniscoid evolution, one which led to ultimate extinction in the Cretaceous. These families illustrate the fundamental palaeoniscoid plan. There are, however, many variations on this theme, and some of these were to give rise to better adapted chondrostean orders in the late Palaeozoic and early Mesozoic. From some of these more advanced chondrostean orders the later holosteans and halecostomes were derived.

After the Lower Trias the occurrence of palaeoniscoids in marine beds is rare and it appears that about the beginning of their decline the palaeoniscoids forsook the seas and entered fresh waters where they had few if any competitors (many of the more advanced chondrosteans such as the redfieldiids also returned to fresh water during the Lower Triassic). By the Middle Trias they are more conspicuous in fresh-water than in marine deposits. In the fresh-water Middle Triassic beds of Australia there are some seven or eight recorded palaeoniscoid genera (Wade 1935), while in similar beds in South Africa and North America several new genera occur (Woodward 1889 ; Broom 1913 ; Gardiner 1966).

The Cheirolepididae, containing but the single genus *Cheirolepis* Agassiz, is a fresh-water family (Middle–Upper Devonian), not far removed from the more normal palaeoniscoid condition except in the possession of minute scales which do not overlap and which closely resemble those of the acanthodians. Another such monogeneric family is the Osorioichthyidae *nov.* from the Devonian of Belgium (Casier 1952, 1954), characterized by a large accessory opercular (in this respect it resembles the later Rhabdolepididae). The Tegeolepididae, which range from the Upper Devonian of North America (Newberry 1888) to the Triassic of Australia (Gardiner 1963), have no fulcral scales, unarticulated rays to the pectoral fins, and small thin scales. The remaining Devonian family, the Stegotrachelidae, is known from marine and fresh-water deposits of Middle and Upper Devonian age and continues into the Lower Carboniferous (Gardiner 1963). It is very close to the main palaeoniscoid stem which was to give rise to the majority of the Carboniferous forms but is exceptional in possessing a pineal foramen. All these four families which arose in the Devonian are end lines independently derived from some hitherto as yet unknown ancestor(s). On the other hand the bulk of the Lower Carboniferous palaeoniscoids form a closely related complex consisting of some twelve families. These are the Carbovelidae, Gonatodidae nov., Gyrolepidotidae nov., Cosmoptychiidae, Acrolepididae, Elonichthyidae, Rhadinichthyidae, Canobiidae, Pygopteridae, Rhabdolepididae, Styracopteridae, and Cryphiolepididae. All possess many features in common and were clearly derived from the same basal stock (one not far removed from the Stegotrachelidae). They all closely adhere to the typical palaeoniscoid condition. From this complex a further thirteen families were subsequently derived—the Brachydegmidae *nov*, Coccocephalichthyidae, Boreolepididae, Boreosomidae *nov*, Palaeoniscidae, Centrolepididae, Coccolepididae, Cosmolepididae *nov*, Amblypteridae, Commentryidae, Dicellopygidae, Aeduellidae and Lawniidae *nov*.

The Brachydegmidae *nov*, Boreolepididae and Coccocephalichthyidae are all too poorly known to establish relationships.

The Palaeoniscidae, Boreosomidae *nov*, Cosmolepididae *nov*, and Centrolepididae all stemmed from an ancestor not too far removed from the Acrolepididae while the Coccolepididae was probably derived from the Palaeoniscidae.

The Amblypteridae, Aedullidae, Commentryidae, Dicellopygidae and Lawniidae *nov* are all related to the Gonatodidae.

The Family Palaeoniscidae includes some ten genera, ranging in time from the Upper Permian to the Upper Trias, and all of which retain the basic palaeoniscoid condition. They are typically fusiform fishes with strongly heterocercal tails, rhomboidal, enamel-covered scales and an oblique suspensorium. The earliest genus is *Palaeoniscum* Blainville (Westoll *in* Aldinger 1937) which ranges from the Upper Permian to the Lower Trias. *Pteronisculus* White (Nielsen 1942) from the Lower Trias of Madagascar, Spitsbergen and Greenland is another typical member, while some of the freshwater palaeoniscoids recorded from the Middle Trias of Australia, such as *Agecephalichthys* Wade, *Myriolepis* Egerton and *Belichthys* Wade (Wade 1935), are also included tentatively in this family. The Palaeoniscidae are close to both the Elonichthyidae and the Acrolepididae, and represent a very conservative stock. The body form, fins and scaling are essentially similar in all three families. The Palaeoniscidae, however, differ from the Elonichthyidae in the development of the cranial roofing bones, in the dorso-anterior development of the preopercular, the enlargement of the suborbital series, the lengthening of the jaws and in the structure of the scales (Aldinger 1937). The Palaeoniscidae differ from the Acrolepididae in the development of the cranial roofing bones, in the more ventral position of the nares, in the greater fragmentation of the infraorbital and suborbital series and in the structure of the scales (Aldinger 1937). Of the two families Elonichthyidae and Acrolepididae, probably the Acrolepididae gave rise to the Palaeoniscidae.

The Centrolepididae contains a single genus *Centrolepis* Egerton which is confined to the marine Lower Lias (Gardiner 1960). It is a fusiform fish with an elongate body, and the fins are of the normal palaeoniscoid pattern with the dorsal opposed to the space between the pelvics and anal. The scales are thick, enamelled and highly ornamented, the suspensorium very oblique and the rostrum pronounced. Apart from the absence of a dermohyal the skull is not dissimilar to that of *Rhadinichthys* or *Palaeoniscum*. In most respects this family has retained the conservative palaeoniscoid structure to the last. It arose from the same stock that gave rise to the Palaeoniscidae but itself gave rise to no other forms.

The Cosmolepididae *nov* is another Lower Liassic marine family, with but one

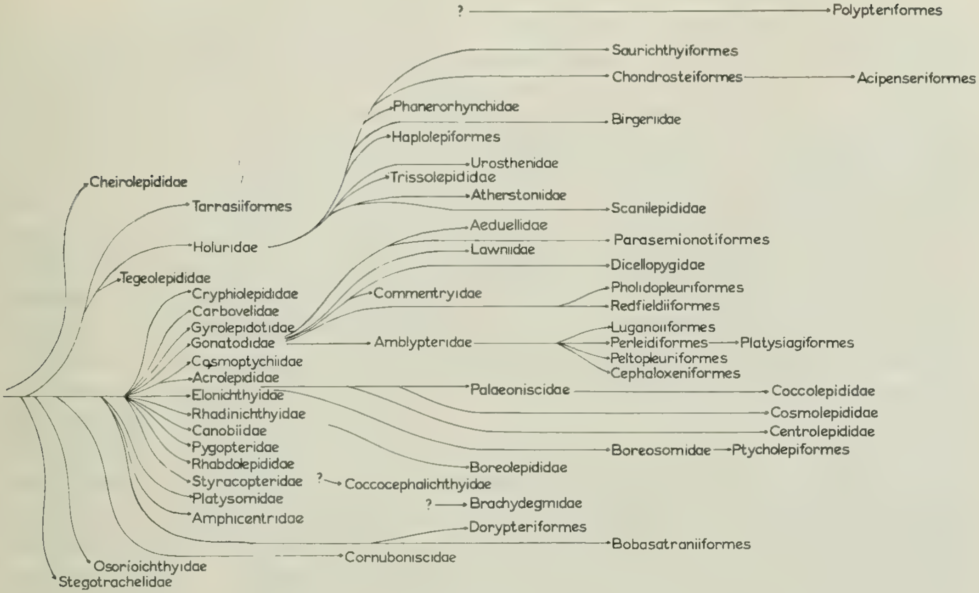
?
Polypteriformes
Saurichthyiformes
Chondrosteiformes
Acipenseriformes
Phanerorhynchidae
Birgeriidae
Haplolepiformes
Urosthenidae
Trissolepididae
Atherstoniidae
Scanilepididae
Cheirolepididae
Tarrasiiformes
Holuridae
Aeduellidae
Lawniidae
Parasemionotiformes
Dicellopygidae
Tegeolepididae
Cryphiolepididae
Carbovelidae
Gyrolepidotidae
Gonatodidae
Commentryidae
Pholidopleuriformes
Redfieldiiformes
Amblypteridae
Luganoiiformes
Perleidiformes
Platysiagiformes
Peltopleuriformes
Cephaloxeniformes
Cosmoptychiidae
Acrolepididae
Palaeoniscidae
Coccolepididae
Elonichthyidae
Cosmolepididae
Rhadinichthyidae
Centrolepididae
Canobiidae
Pygopteridae
Boreosomidae
Ptycholepiformes
Rhabdolepididae
Boreolepididae
Styracopteridae
?
Coccocephalichthyidae
Platysomidae
?
Brachydegmidae
Amphicentridae
Dorypteriformes
Bobasatraniiformes
Cornuboniscidae
Osorioichthyidae
Stegotrachelidae

FIG. 24. Phylogeny of the Chondrostei.

representative, *Cosmolepis* Egerton. One of the characteristics of *Cosmolepis* is that the supraorbital sensory canal posteriorly does not enter the parietal but unites with the infraorbital canal (Watson 1925) (a similar condition is seen in *Brookvalia* Wade, *Acentrophorus* Gill and teleosts). The body is elongate, the dorsal and anal fins long-based and the scales small. It differs from the Palaeoniscidae in the greater length of its jaws and suprascapular, the more oblique suspensorium and the scale structure (Gardiner 1960). In general this family is close to *Palaeoniscum* and, like the Centrolepididae, shared a common ancestor with the Palaeoniscidae.

Finally the Family Coccolepididae (Berg 1940) which ranges from the Lower Lias to the Wealden comprises a single genus *Coccolepis*. The coccolepids are slender fusiform fishes with heterocercal tails, deeply forked in most forms but inequilobate. The suspensorium is very oblique, the scales are thin and deeply imbricating but the overhanging rostrum has been reduced and lost and there is no suborbital series present (Gardiner 1960). *Coccolepis* is very similar to the earlier Palaeoniscidae but differs in the absence of a suborbital series and in the more rounded outline of the opercular series. It was directly derived from the Palaeoniscidae.

These last three families all represent end lines which managed to survive comparatively unchanged from the Palaeozoic and which eventually gave way to the far better adapted holosteans.

The Family Boreosomidae *nov* ranges from the Permian to the Middle Trias (Gardiner 1966*a*). The suspensorium is almost vertical but there is still a pronounced rostrum (Lehman 1952). The tail is strongly forked and the dorsal fin is situated well forward with its anterior border in front of the pelvics ; the orbit is large. *Boreosomus* Stensiö itself was an active midwater to surface swimmer, presumably plankton feeding. The affinities of this family are not at all clear, although it seems possible that it is distantly related to the Palaeoniscidae and probably had its origin in the Acrolepididae. However, what is more certain is what the family gave rise to; Brough (1939) has clearly demonstrated the affinities of the family to the Ptycholepiformes, and there can be little doubt that this later chondrostean order was derived from the Boreosomidae.

The Amblypteridae contains four genera ranging from the Upper Carboniferous to the Lower Permian. Its members are characterized by the large paired fins, upright suspensorium and the single series of teeth in the jaws (Gardiner 1963). The family is derived from the earlier Gonatodidae *nov*. The Amblypteridae have many features in common with the earlier Gonatodidae, in particular the height of the preopercular, the straightening of the suspensorium and the single series of teeth in the jaws. The Amblypteridae differ from the Gonatodidae in that the suspensorium is nearer the vertical, the branchiostegal rays are fewer in number and the head is somewhat deeper. Within the Gonatodidae the genera *Pseudogonatodus* nov. and *Drydenius* Traquair show how the maxilla has grown down around the peg-like teeth, and so lead on to the condition seen in the later genus *Paramblypterus* Sauvage (Amblypteridae) where the maxilla almost encases the teeth. A similar sheathing of the teeth is to be seen in *Aeduella* Westoll (Blot & Heyler 1963) which adds weight to the conclusion that the Aeduellidae were also derived from the Gonatodidae.

The Family Aeduellidae is made up of but two genera, *Aeduella* and *Westollia* White & Moy-Thomas, both from the marine Permian. Both are characterized by an upright, narrow preopercular and a maxilla which has no posterior expanded blade (Westoll 1937). The Aeduellidae resemble the earlier Gonatodidae in body shape, disposition and make-up of the fins, and in the possession of a high preopercular. The Aeduellidae differs from the Gonatodidae in that the suspensorium is inclined forward, in the absence of a suborbital series (although anamestic fragmentation of the preopercular is occurring) and in the reduction of the posterior blade of the maxilla.

The Commentryidae (Gardiner 1963) with its single genus has a more typical palaeoniscoid dentition with a double tooth series including an outer row of larger teeth (Blot 1963). There are several parietal ossifications present and the dorsal fin is situated far back with the anal fin more anteriorly placed. This family, like the Amblypteridae, stemmed from the Gonatodidae. The Commentryidae differ from the Gonatodidae in the more posterior insertion of the dorsal fin, in the fragmentation of the parietals and extrascapulars, and in the possession of a double tooth series.

Close to the Commentryidae is another monogeneric family, the Dicellopygidae, from the fresh-water Lower Trias of Bekker's Kraal, South Africa (Brough 1931). The suspensorium is nearer the vertical and the caudal fin strongly forked and almost equilobate, but the general make-up of the skull is comparable to that of the Commentryidae. The scales are relatively large but the maxilla and cheeks are typically palaeoniscoid. This family represents a fresh-water side line.

From fresh-water deposits of Permian age in North America comes yet another monogeneric family, the Lawniidae *nov* (Wilson 1953). In general *Lawnia* resembles the Amblypteridae, apart from the rather specialized arrangement of its antorbital in relation to the narial opening and in body shape (which is fusiform). However there can be little doubt that this family has been independently derived from the earlier Gonatodidae.

Returning now to the closely related complex of twelve families in the Lower Carboniferous, there are two other families, the Amphicentridae and the Platysomidae (Moy-Thomas 1939) which are not so very far removed from this complex and which unquestionably shared a common ancestry with it. These two families include all the deep bodied palaeoniscoids, from the Lower Carboniferous up to the Triassic.

In all essential features the Amphicentridae and Platysomidae are almost identical with the palaeoniscoids making up this related complex of twelve families, but differ mainly in their body shape. The body is laterally compressed and dorso-ventrally deepened. The differences between these two families and the other palaeoniscoids are merely a question of modification as a result of a change in body shape. The most obvious differences are the shape of the maxilla which is almost triangular, the jaw suspension which is vertical (as in the families Canobiidae, Amblypteridae, Aeduellidae, etc.), the short, deep skull and the elongation of the body scales in the dorso-ventral plane. With the change in slope of the face, the nostrils are borne much higher up than in most palaeoniscoids. The dorsal fin is often considerably elongated, while the heterocercal tail is equilobate in many forms, superficially resembling the homocercal condition seen in more advanced actinopterygians. These two families undoubtedly arose from the same parental palaeoniscoid stock and, although their members flourished throughout the Carboniferous and Permian, only one or maybe two genera survived into the Mesozoic (*Caurichthys* Broom, *Platysomus* Agassiz). The two families are separated mainly on the form of the dentition. The Platysomidae have small, conical, often pointed teeth while the Amphicentridae have a more powerful crushing dentition with tooth plates developed on the coronoids and endopterygoids (Dyne 1939). The Amphicentridae did not survive the Palaeozoic, but the Platysomidae are represented in the Lower Trias by *Caurichthys* and also possibly by the long ranging *Platysomus*. Both families were adapted for browsing among the lagoonal coral reefs and finally succumbed to the rather more highly evolved bobasatranids. It seems probable that the bobasatranids, with their more powerful crushing dentition, came from the same basal stock as the Amphicentridae, while both the Amphicentridae and the Platysomidae were derived from the same ancestral stock which gave rise to the related complex of twelve families.

An important Carboniferous family which has been independently derived from the ancestral palaeoniscoid stock is the Holuridae (Moy-Thomas 1939). In this family the bones of the skull conform to the normal palaeoniscoid condition, but it is in the make-up of the fins that the Holuridae differ markedly from all the other palaeoniscoid lineages. The lepidotrichia of all the fins are articulated but *not* distally bifurcating and there are *no* fulcra present. Further the caudal fin is *not* cleft. The Holuridae gave rise to the Phanerorhynchidae, Birgeriidae, Trissolepididae, Atherstoniidae *nov*, and possibly the Urosthenidae and Scanilepididae, while the later chondrostean orders, Haplolepiformes, Saurichthyiformes and Chondrosteiformes also came of this lineage.

The Phanerorhynchidae are known from a single genus, *Phanerorhynchus* Gill from the Upper Carboniferous (Gill 1923). The skull is much as in the more typical palaeoniscoids, apart from the snout which is drawn out into a distinct rostrum projecting beyond the anterior limits of the lower jaw. The actual arrangement of the snout bones is almost identical to that seen in the Haplolepiformes (Westoll 1944). The body scaling is peculiar and consists of very large scales with prominent ridge scales along the dorsal contour, as in the Holuridae. The fin rays are unarticulated and never bifurcated and there are no fulcral scales (as in the Holuridae). The tail was probably not cleft. This family is not far removed from either the Haplolepiformes or the Chondrosteiformes.

The Family Birgeriidae also contains only one recorded genus, *Birgeria* Stensiö which occurs throughout the marine Trias. It is characterized by the large number of suborbitals in the cheek region (Nielsen 1949). The opercular is triangular, the subopercular splint-like and similar to the succeeding branchiostegal rays. The suspensorium is very oblique. The anterior fin rays are not bifurcated and fulcral scales are absent. Like the Phanerorhynchidae it was derived from the holurid lineage.

The Trissolepididae is composed of two genera—*Sphaerolepis* Frič and *Sceletophorus* Frič, both from the Upper Carboniferous of Czechoslovakia. The suspensorium is upright and the snout rounded. The fin rays of all the fins are relatively few in number, articulated but not bifurcating distally. Fulcral scales are absent and the caudal fin is not truly cleft. The Trissolepididae in all these points resemble the earlier Holuridae from which they were derived.

The Family Atherstoniidae *nov* has been erected to include the genus *Atherstonia* Woodward (Upper Permian–Upper Trias). The fin rays in this family are very numerous, articulated but not distally bifurcating. The family is close to the Trissolepididae.

The Scanilepididae are a Triassic family, characterized by a very long dorsal fin containing seventy rays or more (Aldinger 1937). The skull is typically palaeoniscoid, the suspensorium oblique and it may be related to the earlier Holuridae.

Finally the remaining family of this lineage, the Urosthenidae (Woodward 1931), containing the single genus *Urosthenes* Dana, comes from the Permian of New South Wales. The fins have no fulcral scales but it would appear that some of the rays are bifurcated. The absence of dorsal ridge scales on the tail and the peculiar lobed nature of the unpaired fins make the systematic position of this family exceedingly doubtful.

There is one final palaeoniscoid family which has not as yet been dealt with, the Cornuboniscidae (White 1939), containing the single genus *Cornuboniscus* White from the Upper Carboniferous of Cornwall. The genus is characterized by the large maxillae which meet anteriorly and by the reduced opercular and preopercular. Since it does not appear to be related to any of the families described above, an independent derivation from the ancestral palaeoniscoid stock must be postulated.

Leaving the Palaeonisciformes we move on to more advanced Chondrostean orders which have been derived from them.

Order TARRASIIFORMES

The Order Tarrasiiformes includes a single family, the Tarrasiidae, which has only two genera, *Tarrasius* Traquair from the Lower Carboniferous of Scotland and *Palaeophichthys* Eastman from the Upper Carboniferous of Illinois.

The skull in *Tarrasius* is identical with that seen in some of the more primitive Palaeonisciformes (Moy-Thomas & Dyne 1938), while the scales (which are confined to the posterior region) are similar to those of *Cheirolepis* Agassiz (Moy-Thomas & Dyne 1938). However the body is elongated and resembles that of the recent *Polypterus* Lacépède as do the rounded, fleshy lobed, pectoral fins. The dorsal and anal fins are continuous with the caudal which is diphycercal. The fins have no fulcral scales and the rays are articulated but not distally bifurcated ; in these respects the Tarrasiiformes resemble the Holuridae. The Tarrasiiformes are related to the palaeonisciform family Holuridae and must have shared a common ancestry with that family.

Order HAPLOLEPIFORMES

Again this order is composed of a single family, the Teleopterinidae (Berg 1936, Westoll 1944), from the Upper Carboniferous of Europe and North America.

The order is characterized by the structure of the fins in which the lepidotrichia are stout, few in number and not distally bifurcated. Rather peculiar, large, fulcral scales fringe the fins anteriorly, the cleithrum is considerably expanded ventrally, the opercular apparatus is small, the branchiostegal rays are reduced, and the gulars much expanded. The head is broad and short, and anamestic fragmentation of the preopercular is taking place. From a comparison of the snout and fins it seems clear that the Haplolepiformes are fairly close to the Palaeoniscoid family Phanerorhynchidae and as such were derived from the earlier Holuridae.

Order SAURICHTHYIFORMES

This order was founded (Lehman *in* Grassé 1958) on the single family Belonorhynchidae which contains two genera, *Saurichthys* Agassiz, in which all Triassic forms are placed, and *Saurorhynchus* Reis which contains only two species, both from the Lias.

Saurichthys is a widely occurring genus found in the marine Lower Trias of Spitsbergen, Greenland, Madagascar, Europe and North America and in the fresh water Middle Triassic deposits of Australia. *Saurorhynchus* occurs in the marine Lower and Upper Lias of Europe.

These fishes range in size from a few inches to several feet and are elongate, slender forms with a much produced rostrum (Stensiö 1925 ; Gardiner 1960). The tail is abbreviate-diphycercal and the dorsal fin is situated far back, above the anal. The lepidotrichia exceed the endoskeletal supports in number and long slender ribs are present. Fulcral scales are minute or absent. The squamation is not continuous, usually only four rows of scales are present, one dorsal, one ventral and one lateral on either side supporting the lateral line, otherwise the body is naked [*Saurorhynchus brevirostris* (Woodward)]. The maxilla is typically palaeoniscoid, firmly attached to the preopercular and quadratojugal, and from within to the ectopterygoid and dermopalatine. The suspensorium is almost upright, and the opercular apparatus consists of a single large opercular, the branchiostegal rays being reduced to one or completely wanting. The dentition consists of well-spaced, large, conical teeth, with numerous intervening smaller teeth. These well-armed, extremely long jaws mark the saurichthyids as among the most predaceous of the Triassic actinopterygians. The neurocranium is completely ossified but lacks a basipterygoid proces (Gardiner 1960). The sensory canal system is essentially palaeoniscoid and the nasal bone contains two nasal orifices between which the supraorbital sensory canal passes.

The Saurichthyiformes form a degenerating series, closely related both to the Palaeonisciformes and to the Chondrosteiformes, and like the Chondrosteiformes they are not far removed from the earlier Phanerorhynchidae. *Phanerorhynchus* with its small fins, reduced number of scale rows and pronounced rostrum shows the way by which the Saurichthyiformes could have been derived from the Palaeonisciformes. The Saurichthyiformes although successful in the Triassic, never gave rise to any further forms.

Order CHONDROSTEIFORMES

The Chondrosteiformes, like the Saurichthyiformes, appeared in the Lower Trias [*Errolichthys* (Lehman 1952)] and died out in the Upper Jurassic (Liu & Zhou 1964). However, they appear to have been restricted to a purely marine habitat. The Chondrosteiformes show reduction in both body scaling and skull bones. The scaling is rudimentary and the pectoral fin is devoid of fulcral scales and without articulations. The rostrum is moderately to well developed. The maxilla and opercular bones are reduced, the suspensorium still somewhat backwardly inclined and the suprascapular is much elongated. The tail is heterocercal with a well developed scaly lobe. The unpaired fins are typically palaeoniscoid, the rays more numerous than their supports. The best-known member is *Chondrosteus* Egerton from the Lias of Europe. In this form the mouth is withdrawn behind the projecting rostrum and was probably suctorial as in the Recent sturgeons.

The Chondrosteiformes, like the Saurichthyiformes, were probably derived from the earlier Holuridae (possibly *via* the Phanerorhynchidae) but unlike the Saurichthyiformes they went on to give rise to more recent groups. The Acipenseriformes were derived from the Chondrosteiformes.

Order ACIPENSERIFORMES

The Order Acipenseriformes includes two distinct families, the Acipenseridae and the Polyodontidae. Both these families first occurred in the Upper Cretaceous and are represented today by several genera.

The Family Acipenseridae (sturgeons) is widespread today in both salt and fresh water. The best-known genus is *Acipenser* Linnaeus which is first found in marine, Upper Cretaceous deposits. Reduction in ossification has continued from the condition seen in the Chondrosteiformes until little or no ossification of the internal skeleton remains. The scales, as in the Saurichthyiformes, have been reduced to a few rows of large bony scutes, but the fins are still essentially palaeoniscoid in structure and the tail is heterocercal. *Acipenser* is a bottom feeding scavenger, picking up molluscs, crustaceans, etc.

The Family Polyodontidae or paddle fishes first occurred in the Upper Cretaceous of Montana [*Palaeopsephurus* MacAlpin (1947)]. Today members are found in river systems in North America and China (*Polyodon* Schneider and *Psephurus* Guenther respectively). In this family the rostrum has become very elongated and tactile. The eyes are small and above the anterior end of the upper jaw. The primary jaws are very large and the hyomandibular oblique. The opercular has been lost and the subopercular, still large in *Palaeopsephurus*, is much reduced in the living *Polyodon*. The tail is heterocercal and the unpaired fins much as in the Acipenseridae. The skull bones and body scaling are much reduced. As already stated, this order was derived from the earlier Chondrosteiformes.

Order POLYPTERIFORMES

This order is only known from two Recent genera, *Polypterus* Lacépède and *Erpetoichthys* Smith which are confined to the rivers and swamps of tropical Africa.

It has been fashionable of recent years (Lehman *in* Grassé 1958) to separate the Polypteriformes from the Chondrostei and place them in their own Subclass, the Brachiopterygii. However, they retain so many obviously palaeoniscoid features that I do not consider this justified. The scales are typically " ganoid ", the sensory canal system is much as in the higher chondrosteans, and in some respects as in the holosteans. The preopercular is still very much palaeoniscoid in make-up, although its intimate connection with the maxilla has been lost. The snout is primitive and the large number of individual bones above the preopercular is yet another chondostrean character. *Polypterus* shows many discrepancies from the normal chondrostean pattern, especially in the nature of the pectoral fins, the dorsal fins and the tail, but the chondrostean *Tarrasius* from the Lower Carboniferous possesses a continuous dorsal fin and a diphycercal tail. *Polypterus* is merely a much modified chondrostean survivor for which, unfortunately, the connecting links are as yet missing.

Order PERLEIDIFORMES

The Perleidiformes represent a big step forward in chondrostean evolution, and in many respects resemble the contemporaneous holosteans. They were a very successful order, containing some twenty-two or more genera from three families. The earliest members are recorded from the Lower Triassic and after a brief but interesting history the order died out at the end of the Trias due to increasingly unsuccessful competition with the more advanced holosteans.

The origins of this order are somewhat uncertain although it would seem that it was derived from the Amblypteridae. Like the Amblypteridae the Perleidiformes have a high preopercular, which in both *Paramblypterus* and *Perleidus* (Stensiö 1921) shows anemestic fragmentation dorsally. The Perleidiformes still possess typically " ganoid " scales but the general structure of the more advanced members is much closer to the holostean than to the palaeoniscoid condition. The heterocercal tail is modified to a hemiheterocercal condition while the lepidotrichia of the unpaired fins come to equal their endoskeletal supports in number.

The Family Colobodontidae (Stensiö 1916) was essentially a marine one, but with a few fresh-water members. In this family the lepidotrichia of the unpaired fins equal the endoskeletal supports in number and are only articulated distally, the proximal portion being entire. The rays are stiff and bifurcated distally. The fins closely resemble those of holosteans. The suspensorium is upright and the preopercular high and large. *Colobodus* Agassiz from the Middle to Upper Trias was a large, marine form, reaching a length of between two and three feet, and probably a bottom dweller like the present day Cod. Its dentition consists of partly pointed and partly crushing teeth, and this type of dentition marks it off sharply from the Redfieldiiformes. *Perleidus* Deecke ranges throughout the marine Trias and is a more typical member of this family, while *Dollopterus* Abel, *Thoracopterus* Broom, *Gigantopterus* Abel and *Albertonia* Gardiner (1966) on the other hand, all possess enlarged pectoral fins, suggestive of the modern teleostean flying fishes.

The Family Aetheodontidae (Brough 1939) shows some similarity to the Colobodontidae, especially in the form of the dentition, the skull roof, opercular apparatus and preopercular, and it would appear logical to include it here in the Perleidiformes. There is a single genus *Aetheodontus* Brough which occurs in the marine Middle to Upper Trias (Brough 1939). The suspensorium is vertical, the dorsal and pelvic fins remote and the rays few in number. The tail is hemiheterocercal with a short scaly lobe, and the scales are small, stout and numerous.

Finally the Family Cleithrolepididae which is both marine and fresh-water and confined to the Trias. Members are recorded from the Lower Trias of Australia, the Middle Trias of South Africa, the Middle and Upper Trias of Germany and the Upper Trias of England. The fins are much as in the colobodontids except that in the anterior portion of the dorsal fin in *Cleithrolepidina* Berg the lepidotrichia outnumber their supports (Brough 1931). The chief characteristics of this family are the very much deepened form of the trunk and the weak mandible which bears minute teeth. The opercular is smaller than the subopercular, the suspensorium is upright and the preopercular is high, similar to that of some colobodontids (*Meidiichthys* Brough). The family retains some palaeoniscoid characters in common with the Colobodontidae and in the present state of knowledge can most usefully be associated with the Colobodontidae and the Aetheodontidae in the order Perleidiformes.

Order PELTOPLEURIFORMES

This order shows some points of similarity to the Colobodontidae (cf. *Meridensia* Stensiö (1921)) and clearly came from the same ancestral stock. Both *Peltopleurus* Kner and *Meridensia* have a similar body shape, almost identical fins and comparable skulls. *Peltopleurus* differs in the great elongation of its flank scales and in the make up of the snout (Brough 1939). The order contains two families, both of which are confined to the marine Upper Trias. Its members are small fishes with an upright suspensorium, large orbits and a hemiheterocercal tail. The tail is strongly forked, almost symmetrical externally, and with a reduced scaly lobe. The unpaired fins are small with relatively few rays and the rays are unjoined proximally (apart from the caudal) but distally bifurcated. The bones of the head are essentially palaeoniscoid, particularly the maxilla, but the suspensorium is upright. The opercular is large and the preopercular is high and shows anamestic fragmentation, as in the Colobodontidae. The dentition is weak, the scales few in number and those of the flank greatly elongated dorso-ventrally as in the Cephaloxeniformes.

The Family Peltopleuridae (Brough 1939) contains two genera, *Peltopleurus* and *Placopleurus* Brough from the Upper Trias of Besano. These were probably plankton feeders, since their teeth are minute.

The Family Habriochthyidae *nov.* has only one genus *Habroichthys* Brough (1939) and this also comes from the Upper Trias of Besano. *Habriochthys* differs from the Peltopleuridae in having but a single row of greatly deepened scales on the flank, while the tail looks completely homocercal. Further the scaling posteriorly finishes in an enlarged, symmetrical, semicircular scale.

Order CEPHALOXENIFORMES

This order contains one family, the Cephaloxenidae with but a single genus, *Cephaloxenus* Brough, which ranges from the marine Middle to Upper Trias (Brough 1939).

Cephaloxenus is a small fish of deeply fusiform shape and with massive, thick skull bones The fins have relatively few, stiff rays, which are large and unarticulated but distally bifurcated. The suspensorium is slightly inclined backwards, the opercular large and the subopercular small. The tail is hemiheterocercal and almost symmetrical externally, with the scaly lobe reduced. The scales are stout, few in number, those of the flank being greatly elongated dorso-ventrally. The preopercular, although not large, is still high, but the maxilla is rounded posteriorly and relatively broad anteriorly and the orbit is small. The deepened body, large fins, heavily armoured head and crushing dentition shows *Cephaloxenus* to have been a bottom dweller, presumably feeding on molluscs, crustaceans, etc. The affinities of this order remain obscure, but in general body form and elongation of the flank scales there is some similarity to the previous order.

Order LUGANOIIFORMES

The Order Luganoiiformes includes the single Family Luganoiidae which is represented by two genera from the marine Middle and Upper Trias (Brough 1939). The members are small, very advanced chondrosteans with fusiform bodies and somewhat dorso-ventrally compressed heads. The skull is characterized by a certain amount of fusion of the roofing bones. Thus in *Luganoia* Brough the parietals, dermopterotics and dermosphenotics have fused into a posterior bony plate and the frontals have also fused into an anterior plate which is distinctly narrow anteriorly. In *Besania* Brough all these elements have fused into a single bony sheet. The opercular and subopercular are of approximately the same size and form a semicircular opercular cover, with a straight anterior border. The suspensorium is inclined forwards as in the semionotids (holosteans), but the preopercular is still large and high as in the Colobodontidae and the Peltopleuriformes. The maxilla however is reduced in size and has lost its intimate connection with the other cheek bones, particularly the preopercular, and has migrated anteriorly to resemble closely that of the more advanced semionotids. The lepidotrichia of the unpaired fins are few in number and presumably, equalled their endoskeletal supports. The individual rays are stiff and unarticulated proximally. The hemiheterocercal tail is markedly rounded and its scale lobe very short. The lower jaw has the beginnings of a coronoid process. The scales are thick, enamelled and those of the anterior flank region elongated dorso-ventrally. These fishes stand on the threshold of the holostean grade of evolution but still retain sufficient chondrostean characters to be regarded as among the most advanced chondrosteans, just falling short of the holostean grade. The obvious chondrostean characters include the lack of an interopercular and the retention of a large plate-like preopercular with a series of triangular bones above its dorsal extremity. This order provides another example of parallel evolution.

Both *Luganoia* and *Besania* have pointed teeth along the jaw margins and although the gape is somewhat restricted they were probably quite voracious, surface to mid-water feeders. The Luganoiiformes have several features in common with the Peltopleuriformes, in particular the greatly elongated flank scales and the high, large preopercular, which is dorsally fragmented. This order shared a common origin with the Perleidiformes, Peltopleuriformes and Cephaloxeniformes.

Order PLATYSIAGIFORMES

Another order composed of a single family, the Platysiagidae, containing only one genus, *Platysiagum* Egerton. *Platysiagum* extends from the Middle Trias to the Lower Lias (Gardiner 1960, 1966*a*) and is essentially a marine form. It is of elongate fusiform shape with a deeply forked, equilobate tail (hemiheterocercal). The paired fins are holostean in structure, as in the previous order, and are of moderate size. All the fins have numerous small fulcra, and the lepidotrichia are stout, bifurcating and only distally articulated. The mandible has a broad coronoid process and the dentition consists of a series of large, conical, pointed teeth, interspersed with numerous, irregularly arranged smaller teeth, suggestive of a predaceous habit. The suspensorium is vertical, the maxilla palaeoniscoid in shape and the preopercular high, broad and dorsally fragmented, similar to that of the Colobodontidae. The Platysiagiformes have basically the same skull structure as the Colobodontidae but differ in possessing an incipient interopercular and in the absence of a suborbital series. This order was probably derived from the Colobodontidae (Perleidiformes) and represents another chondrostean order which has moved independently towards the holostean grade of structure.

Order REDFIELDIIFORMES

The Order Redfieldiiformes includes the single family Dictyopygidae, which for a long time has been associated with the Colobodontidae in the Order Perleidiformes.

The Redfieldiiformes, however, can be distinguished from the Perleidiformes by the excess of rays over radials in both the dorsal and anal fins and in having often only one modified branchiostegal ray.

The origins of this order are somewhat obscure although the contemporaneous Dicellopygidae appears to have been derived from the same palaeonisciform stock (Gonatodidae–Commentryidae).

The Family Dictyopygidae is a fresh-water group, well represented in the Lower and Middle Triassic fresh-water beds of South Africa, Australia and North America (Brough 1931). The most primitive members of the Dictyopygidae exhibit the more conservative palaeoniscoid condition apart from the tail which is now hemiheterocercal. In the main the redfieldiids differ from the perleidids in that the dermal rays of the fin are more numerous than the endoskeletal supports and are also completely articulated. The snout still has the prominent palaeoniscoid rostrum and the rostro-premaxillo-antorbital is still a single bone in the primitive members. The suspensorium is oblique. However, Brough (1931) has shown that within the redfieldiids structural changes were taking place, so that the more advanced forms had come to resemble the perleidids much more closely. The suspensorium straightens and the lepidotrichia of the pectoral fin are undivided proximally, the caudal fin becomes less and less heterocercal and the lepidotrichia of the paired fins come to almost equal the endoskeletal supports. Of the sixteen or more described genera, eight are recorded from Australia and another five from South Africa. *Redfieldius* Hay is well known from the Upper Trias of South Africa and North America. The early redfieldiids are thus very similar to the predaceous palaeoniscoids, both in body shape, fin structure and dentitition, and presumably had very similar habits.

Order PHOLIDOPLEURIFORMES

This order ranges from the Lower to Upper Trias. It contains one family, the Pholidopleuridae, three members of which are marine and the fourth fresh-water (*Macroaethes* Wade). The pholidopleurids are small to moderately long, slender fishes. The dorsal and anal fins are far back, the origin of the anal being anterior to that of the dorsal. The lepidotrichia of the unpaired fins are more numerous than the endoskeletal supports and all are articulated and distally bifurcated. The tail is hemiheterocercal, deeply cleft and with a reduced scaly lobe. The suspensorium is almost vertical to moderately oblique, the orbit large and the preopercular high and perleidid in make up. The frontals are very large and the rostrum is blunt. The parietals are considerably subdivided into a series of elements. The maxilla has the normal palaeoniscoid proportions, the teeth are small and pointed and the scales thin. *Australosomus* Piveteau from the Lower Triassic, marine deposits of Madagascar, Greenland and Spitsbergen was a wide-ranging species and it is also recorded from the Lower Trias of Tanzania, while *Macroaethes* Wade is confined to Middle Triassic, fresh-water deposits of Australia. This again is another chondrostean order whose affinities remain obscure, but which possibly originated from the same palaeoniscoid stock as the Redfieldiiformes.

Order PARASEMIONOTIFORMES

This order is probably the most important of the more advanced chondrostean orders since it provides the almost ideal stepping-stone to the more advanced holosteans and halecostomes. The order contains two families, the Parasemionotidae and the Tungusichthyidae, which are confined to the marine Lower Trias.

The Family Tungusichthyidae, containing the single genus *Tungusichthys* Berg (Berg 1941) from the Lower Trias of the Tunguska Coal Basin, Siberia, is not well known. The caudal fin still has a pronounced scaly lobe but superficially tends towards the homocercal condition, being only weakly cleft. The fins are distinctly holostean in make-up with few rays and these are bifurcated but only distally articulated. The suspensorium is vertical and the preopercular narrow as in the caturids ; in this respect it differs from the Parasemionotidae. The maxilla is thin and reduced, very much holostean in appearance and with a supramaxillary in articulation ; the interopercular is small.

The Family Parasemionotidae contains eight genera from the Lower Trias of Madagascar and Greenland. They represent a fairly uniform group but with considerable variation in the preopercular and snout regions (Lehman 1952).

Apart from the skull, the Parasemionotidae are completely holostean, although the scaly lobe of the hemiheterocercal tail still extends almost halfway along the dorsal lobe. The body shape, size, scaling and nature of the paired and unpaired fins are all distinctly holostean and halecostome. In the skull the roofing bones correspond in basic structure and arrangement to those of the early holosteans and halecostomes. In the cheek region the maxilla is freed from the preopercular while the opercular series includes a true interopercular. In both these features the Parasemionotidae closely approach the holosteans. Only in the size and shape of the preopercular and absence of a true suborbital series do the Parasemionotidae fall short of the holostean and halecostome grades. The preopercular is still large and broad medially and would need to become more curved antero-ventrally and broadened in that region to approach the condition found in the halecostomes. However, Lehman (1952) has shown that within the Parasemionotidae suborbitals are being formed by anamestic fragmentation of the anterior part of the preopercular. Therefore, he concludes that the Parasemionotidae are probably ancestral to the caturids. Further, Gardiner (1960) has shown the remarkable similarity that exists between the Parasemionotidae on the one hand and the halecostomes on the other.

The actual origin of the Parasemionotiformes is less clear. Of the known chondostrean families the Aeduellidae (Palaeonisciformes) look the most likely ancestors. The family includes the two genera *Aeduella* Westoll and *Westollia* White & Moy-Thomas from the Lower Permian of Autun and Thuringia respectively. These are characterized by the upright nature of the suspensorium, the reduction of the posterior expanded portion of the maxilla, and the shape and size of the preopercular. The body is of the right shape and proportions to have given rise to the Parasemionotiformes although the fins are distinctly palaeoniscoid. There is no interopercular. Thus it seems that the Aeduellidae and the Parasemionotiformes shared a common ancestry in the upper Carboniferous.

Order PTYCHOLEPIFORMES

Members of this order are first encountered in the Middle Trias and the order survived into the Upper Lias. The order is represented by a single family, the Ptycholepididae, containing the single genus *Ptycholepis* Agassiz.

Ptycholepis is a marine form and ranges in size from small to large (some 60 cm.). It is elegantly fusiform with an acutely pointed snout (Gardiner 1960). The caudal fin is deeply forked and hemiheterocercal. The pectoral and pelvic fins are well developed, the dorsal and anal fins are triangular, the former opposed to the pelvics, the latter smaller and remote. The lepidotrichia of the unpaired fins are few in number and completely articulated and distally bifurcated, nearly equalling their endoskeletal supports in number. The suspensorium is almost vertical, the gape wide and the orbit large. The dentition consists of two series of small, close-set teeth and these fishes were presumably mid-water, plankton feeders. The frontals are large and elongate, making up the major portion of the skull roof. The skull roofing bones are distinctly ornamented with high ridges of enamel. The snout is produced into a blunt rostrum with a prominent postrostral present. The opercular is large and quadrangular, the scales thick, longer than wide and much elongated in the ventral region.

Because of the holostean-like character of the body and fins, this genus has in the past been grouped in the Holostei, but the absence of an interopercular, the possession of a palaeoniscoid-type maxilla and preopercular (covered with suborbitals in later species) and other obvious chondrostean characters of the skull, such as the snout, show that *Ptycholepis* is a representative of yet another independent line from the palaeoniscoids, which has not yet quite reached the holostean level. Brough (1939) has shown that the Ptycholepiformes can be directly derived from the earlier Boreosomidae.

Order BOBASATRANIIFORMES

The bobastraniids form a compact little group found only in the marine Lower Trias. The single Family Bobasatraniidae has representatives from Spitsbergen, Madagascar, Greenland and North America.

The bobasatraniids resemble the later pycnodonts in many respects but are in no way related to them. The bobasatraniids are an offshoot from the same palaeoniscoid stock which gave rise to the amphicentrids, and they died out without giving rise to any other group. In general body-form the bobasatraniids resemble the earlier Amphicentridae, particularly in the make-up of the shoulder girdle and the unpaired fins and in the much deepened, laterally compressed body. The lepidotrichia of the fins are slightly more numerous than the endoskeletal supports and the dorsal and anal fins are long as in some species of *Platysomus* Agassiz. However the median fins are holostean in form while the opercular apparatus is peculiar. The opercular is small with a much expanded preopercular plate below it and with the branchiostegal rays completely reduced. The clavicle has been lost.

Bobasatrania White (1932) has a modified crushing dentition reminiscent of that seen in *Chirodus*. The suspensorium is upright, the gape small, the pectoral fins long and the pelvics wanting. The dorso-ventrally deepened body, strongly forked heterocercal tail, long dorsal and anal fins and crushing dentition suggest that this was a browsing form probably feeding close inshore amongst corals.

Order DORYPTERIFORMES

The Order Dorypteriformes includes the family Dorypteridae which is represented by the single genus *Dorypterus* Germar from the marine Upper Permian (Gill 1925 ; Liu & Tseng 1964). *Dorypterus* shows many points of similarity to the Bobasatraniiformes and, like this order, was probably derived from the earlier Amphicentridae. There are close relationships between the axial skeleton and fin skeleton of *Dorypterus* and *Bobasatrania* White ; the expanded sinuous axonosts are in contact with one another, while the development of the body axis of the caudal fin is more or less identical in both. The bones of the upper jaw are similarly developed in *Dorypterus* and *Bobasatrania* and the pectoral girdles show many likenesses. However, despite these few similarities there are many divergent features ; no known bobasatraniid shows the extreme modifications of the skull found in *Dorypterus* and likewise the body of *Dorypterus* is not completely covered with thick scales (as in bobasatraniids). The scaling is reduced to the anterior portion of the trunk in *Dorypterus*. It would appear that the dorypterids and bobasatraniids must have come from the same early amphicentrid-like stock but both lines soon died out.

IV. CLASSIFICATION OF THE CHONDROSTEI

Class *ACTINOPTERYGII*

Subclass *CHONDROSTEI*

Order Palaeonisciformes
- Family Cheirolepididae Pander 1860
  - *Cheirolepis* Agassiz 1835
- Family Stegotrachelidae Gardiner 1963
  - *Stegotrachelus* Woodward & White 1926, *Moythomasia* Gross 1950, *Orvikuina* Gross 1953, *Kentuckia* Rayner 1951
- Family Osorioichthyidae nov.
  - *Osorioichthys* Casier 1954 (*Stereolepis* Casier 1952, *Stereolepidella* Whitley 1954)
- Family Tegeolepididae Romer 1945
  - *Tegeolepis* Miller 1892 (*Actinophorus* Newberry 1888), ?*Apateolepis* Woodward 1890, ?*Megapteriscus* Wade 1935, ?*Elpisopholis* Woodward 1908
- Family Carbovelidae Romer 1945
  - *Carboveles* White 1927, *Phanerosteon* Traquair 1881
- Family Gonatodidae nov.
  - *Gonatodus* Traquair 1877, *Drydenius* Traquair 1890, *Pseudogonatodus* nov.
- Family Gyrolepidotidae nov.
  - *Gyrolepidotus* Rohon 1889, *Palaeobergia* Matveeva 1958

Family COSMOPTYCHIIDAE Gardiner 1963
Watsonichthys Aldinger 1937, *Cosmoptychius* Traquair 1877

Family ACROLEPIDIDAE Aldinger 1937
Acrolepis Agassiz 1833, *Acropholis* Aldinger 1935, *Acrorhabdus* Stensiö 1921, *Hyllingea* Aldinger 1935, *Plegmolepis* Aldinger 1937, *Reticulolepis* Aldinger 1937, *Mesonichthys* Gardiner 1963

Family ELONICHTHYIDAE Aldinger 1937
Elonichthys Giebel 1848 (*Ganacrodus* Owen 1867, *Propalaeoniscus* Pomel 1853), *Namaichthys* Gürich 1923

Family RHADINICHTHYIDAE Romer 1945
Rhadinichthys Traquair 1877, *Cycloptychius* Young 1866, *Rhadinoniscus* White 1937, *Aetheretmon* White 1927, *Strepheoschema* White 1927, *Mentzichthys* Jubb 1965, *Eurylepidoides* Case 1935, *Ganolepis* Woodward 1893

Family CANOBIIDAE Aldinger 1937
Canobius Traquair 1881, *Mesopoma* Traquair 1890, *Whiteichthys* Moy-Thomas 1942, ?*Aldingeria* Moy-Thomas 1942

Family PYGOPTERIDAE Aldinger 1937
Nematoptychius Traquair 1875, *Pygopterus* Agassiz 1833

Family RHABDOLEPIDIDAE Gardiner 1963
Rhabdolepis Troschel 1857

Family STYRACOPTERIDAE Moy-Thomas 1939
Styracopterus Traquair 1890 (*Fouldenia* White 1927), *Benedenius* Traquair 1878 (*Benedenichthys* Traquair 1890)

Family CRYPHIOLEPIDIDAE Moy-Thomas 1939
Cryphiolepis Traquair 1881

Family AMPHICENTRIDAE Moy-Thomas 1939
Chirodus M'Coy 1848 (*Amphicentrum* Young 1866, *Cheirodus* M'Coy 1855, *Hemicladodus* Davis 1884), *Cheirodopsis* Traquair 1881, *Eurynothus* Agassiz 1834 (*Eurinotus* Agassiz 1836, *Euronotus* Agassiz 1835, *Eurunotus* Pander 1860, *Eurynotus* Agassiz 1834, *Notaemon* Gistl 1848, *Plectrolepis* Egerton 1850), *Eurynotoides* Berg 1940, *Paraeurynotus* Chabakov 1927, *Globulodus* Münster 1842 (*Eurysomus* Young 1866, *Lekanichthys* Brough 1934), *Proteurynotus* Moy-Thomas & Dyne 1938, ?*Tompoichthys* Obruchev 1964

Family PLATYSOMIDAE Young 1866
Platysomus Agassiz 1833 (*Stromateus* Blainville 1818), *Mesolepis* Young 1866 (*Pododus* Agassiz 1844), *Paramesolepis* Moy-Thomas & Dyne 1938, *Wardichthys* Traquair 1875, *Caruichthys* Broom 1913

Family HOLURIDAE Moy-Thomas 1939
Holurus Traquair 1881, *Holuropsis* Berg 1947, *Palaeoniscinotus* Rohon 1890, *Peleichthys* Broom 1913, *Disichthys* Broom 1913

Family CORNUBONISCIDAE White 1939
Cornuboniscus White 1939

Family PHANERORHYNCHIDAE Stensiö 1932
Phanerorhynchus Gill 1923

Family TRISSOLEPIDIDAE Frič 1893
Sphaerolepis Frič 1877 (*Trissolepis* Frič 1893), *Sceletophorus* Frič 1894 (*Phanerosteon* Frič 1894, *Gymnoniscus* Berg 1936)

Family BIRGERIIDAE Aldinger 1937
Birgeria Stensiö 1919 (*Xenesthes* Jordan 1907), *Ohmdenia* Hauff 1953

Family ATHERSTONIIDAE nov.
Atherstonia Woodward 1889 (*Hypterus* Owen 1876, *Broometta* Chabakov 1928)

Family UROSTHENIDAE Woodward 1931
Urosthenes Dana 1848

Family SCANILEPIDIDAE Romer 1945
Scanilepis Aldinger 1935, *Evenkia* Berg 1941

Family AMBLYPTERIDAE Romer 1945
Amblypterus Agassiz 1833 (*Aedua* Sauvage 1890, *Archaeonichthys* Whitley 1940, *Archaeoniscus* Sauvage 1890, *Leiolepis* Goldenburg 1873), *Paramblypterus* Sauvage 1888 (*Amblypterops* Sauvage 1889, *Cosmopoma* Sauvage 1889, *Dipteroma* Sauvage 1889, *Geomichthys* Sauvage 1889), *Amblypterina* Berg 1940, *Tholonotus* Dunkle & Schaeffer 1956

Family COMMENTRYIDAE Gardiner 1963
Commentrya Sauvage 1888 (*Elaveria* Sauvage 1888)

Family LAWNIIDAE nov.
Lawnia Wilson 1953

Family DICELLOPYGIDAE Romer 1945
Dicellopyge Brough 1931, ?*Aneurolepis* White & Moy-Thomas 1941 (*Urolepis* Bellotti 1857)

Family AEDUELLIDAE Romer 1945
Aeduella Westoll 1937, *Westollia* White & Moy-Thomas 1940 (*Lepidopterus* Pholig 1892)

Family BOREOLEPIDIDAE Aldinger 1937
Boreolepis Aldinger 1937

Family PALAEONISCIDAE Vogt 1852
Palaeoniscum Blainville 1818 (*Eupalaeoniscus* Rzchak 1881, *Palaeoniscus* Agassiz 1833, *Palaeothrissum* Blainville 1818, *Palaeomuzon* Weigelt 1930), *Pteronisculus* White 1933 (*Glaucolepis* Stensiö 1921), *Agecephalichthys* Wade 1935, *Myriolepis* Egerton 1864, *Trachelacanthus* Fischer de Waldehim 1850, *Gyrolepis* Agassiz 1833, ?*Gyrolepidoides* Cabrera 1944, *Turseodus* Leidy 1857, *Belichthys* Wade 1935, ?*Progyrolepis* Frič 1894, ?*Challaia* Rusconi 1946, *Leptogenichthys* Wade 1935

Family COSMOLEPIDIDAE nov.
Cosmolepis Egerton 1854 (*Oxygnathus* Egerton 1854, *Thrissonotus* Agassiz 1844)

Family CENTROLEPIDIDAE Gardiner 1960
Centrolepis Egerton 1858

Family COCCOLEPIDIDAE Berg 1940
  Coccolepis Agassiz 1844, *Browneichthys* Woodward 1889, *Sunolepis* Liu 1957, *Pteroniscus* Chekker 1848
Family COCCOCEPHALICHTHYIDAE Romer 1945
  Coccocephalichthys Whitley 1940 (*Coccocephalus* Watson 1925, *Cocconiscus* White & Moy-Thomas 1940)
Family BRACHYDEGMIDAE nov.
  Brachydegma Dunkle 1939
Family BOREOSOMIDAE nov.
  Boreosomus Stensiö 1921 (*Diaphorognathus* Brough 1933), *Mesembroniscus* Wade 1935
Order TARRASIIFORMES
  Family TARRASIIDAE Traquair 1881
    Tarrasius Traquair 1881, *Palaeophichthys* Eastman 1907.
Order HAPLOLEPIFORMES
  Family TELEOPTERINIDAE Berg 1936
    Haplolepis Miller 1892 (*Eurylepis* Newberry 1857, *Mecolepis* Newberry 1856, *Mekolepis* Newberry 1857), *Pyritocephalus* Frič 1894 (*Teleopterina* Berg 1936)
Order SAURICHTHYIFORMES
  Family BELONORHYNCHIDAE Woodward 1888
    Saurichthys Agassiz 1834 (*Belonorhynchus* Bronn 1858, *Giffonus* Costa 1862, *Ichthyorhynchus* Bellotti 1857, *Stylorhynchus* Martin 1873), *Saurorhynchus* Reis 1892 (*Belonostomus* Agassiz 1844, *Belonorhynchus* Bronn 1858, *Acidorhynchus* Stensiö 1925, *Gymnosaurichthys* Berg 1940)
Order CHONDROSTEIFORMES
  Family CHONDROSTEIDAE Traquair 1877
    Chondrosteus Egerton 1858, *Gyrosteus* Morris 1854, *Stichopterus* Reis 1909, *Strongylosteus* Jaekel 1929
  Family ERROLICHTHYIDAE Lehman 1952
    Errolichthys Lehman 1952, *Psilichthys* Hall 1900
  Family PEIPIAOSTEIDAE Liu & Zhou 1965
    Peipiaosteus Liu & Zhou 1965
Order ACIPENSERIFORMES
  Family ACIPENSERIDAE Bonaparte 1831
    Acipenser Linnaeus 1758, *Huso* Brandt 1833, *Kessleria* Bogdanon 1882 (*Hemiscaphirhynchus* Berg 1911, *Pseudoscaphirhynchus* Nicolsky 1900), *Protoscaphirhynchus* Wilimovsky 1956, *Scaphirhynchus* Heckel 1835
  Family POLYDONTIDAE Bonaparte 1838
    Polyodon Schneider 1801, *Palaeopsephurus* MacAlpin 1947, *Pholidurus* Woodward 1889, *Psephurus* Guenther 1873, *Crossopholis* Cope 1883
Order POLYPTERIFORMES
  Family POLYPTERIDAE
    Polypterus Sainte-Hilaire 1802 (Lacépède 1803), *Erpetoichthys* Smith 1865 (*Calamoichthys* Smith 1866)

Order PERLEIDIFORMES
  Family COLOBODONTIDAE Stensiö 1916
    Colobodus Agassiz 1844, *Crenolepis* Carus 1888 (*Crenilepis* Dames 1888, *Crenilepoides* Strand 1929), *Meridensia* Stensiö 1916, *Perleidus* Alessandri 1910, ?*Thoracopterus* Bronn 1858, ?*Gigantopterus* Abel 1906, *Meidiichthys* Brough 1931, *Mendocinichthys* Whitley 1953 (*Mendocinia* Bordas 1944), *Tripelta* Wade 1940, *Chrotichthys* Wade 1940, *Zeuchthiscus* Wade 1940, *Pristisomus* Woodward 1890, *Manlietta* Wade 1935, *Procheirichthys* Wade 1935, *Dimorpholepis* Teixeira 1947, *Engycolobodus* Oertle 1927, *Dollopterus* Abel 1906, *Albertonia* Gardiner 1966
  Family AETHEODONTIDAE Brough 1939
    Aetheodontus Brough 1939
  Family CLEITHROLEPIDIDAE Wade 1935
    Cleithrolepis Egerton 1864, *Cleithrolepidina* Berg 1955, *Hydropessum* Broom 1909, *Dipteronotus* Egerton 1854
Order LUGANOIIFORMES
  Family LUGANOIIDAE Brough 1939
    Luganoia Brough 1939, *Besania* Brough 1939
Order PELTOPLEURIFORMES
  Family PELTOPLEURIDAE Brough 1939
    Peltopleurus Kner 1866, *Placopleurus* Brough 1939
  Family HABROICHTHYIDAE nov.
    Habroichthys Brough 1939
Order CEPHALOXENIFORMES
  Family CEPHALOXENIDAE Brough 1939
    Cephaloxenus Brough 1939
Order PLATYSIAGIFORMES
  Family PLATYSIAGIDAE Brough 1939
    Platysiagum Egerton 1872
Order REDFIELDIIFORMES
  Family DICTYOPYGIDAE Hay 1889
    Redfieldia Hay 1899 (*Catopterus* Redfield 1837), *Dictyopyge* Egerton 1847, *Daedalichthys* Brough 1931, *Sakamenichthys* Nauche 1959, *Helichthys* Broom 1909, *Atopocephala* Brough 1934, *Brookvalia* Wade 1935, *Beconia* Wade 1935, *Dictyopleurichthys* Wade 1935, *Geitonichthys* Wade 1935, *Molybdichthys* Wade 1935, *Phlyctaenichthys* Wade 1935, *Schizurichthys* Wade 1935, *Ischnolepis* Haughton 1934, *Sinkiangichthys* Liu 1958, *Pseudobeconia* Bordas 1944, ?*Rushlandia* Bock 1959
Order PHOLIDOPLEURIFORMES
  Family PHOLIDOPLEURIDAE Wade 1932
    Australosomus Piveteau 1930, *Pholidopleurus* Bronn 1858, *Macroaethes* Wade 1932, *Arctosomus* Berg 1941 (*Neavichthys* Whitley 1951)
Order PTYCHOLEPIFORMES
  Family PTYCHOLEPIDIDAE Brough 1939
    Ptycholepis Agassiz 1833

- Order DORYPTERIFORMES
  - Family DORYPTERIDAE Gill 1925
    - *Dorypterus* Germar 1842
- Order BOBASATRANIIFORMES
  - Family BOBASATRANIIDAE Stensiö 1932
    - *Bobasatrania* White 1932 (*Lambeichthys* Lehman 1956), *Ecrinesomus* Woodward 1910
- Order PARASEMIONOTIFORMES
  - Family PARASEMIONOTIDAE Stensiö 1932
    - *Parasemionotus* Piveteau 1929, *Stensionotus* Lehman 1952, *Watsonulus* Brough 1939, *Jacobulus* Lehman 1952, *Thomasinotus* Lehman 1952, *Ospia* Stensiö 1932, *Broughia* Stensiö 1932, *Helmolepis* Stensiö 1932
  - Family TUNGUSICHTHYIDAE Berg 1941
    - *Tungusichthys* Berg 1941

Chondrostei incertae sedis

Anaglyphus Rzehak 1881, *Anatoia* Rusconi 1946, *Caminchaia* Rusconi 1946, *Cenchrodus* Meyer 1847, *Cenechoia* Rusconi 1946, *Cephaliscus* Whitley 1940 (*Cephalacanthus* Beyrich 1848), *Echentaia* Rusconi 1946, *Guaymayenia* Rusconi 1946, *Hemilopas* Meyer 1847, *Neochallaia* Rusconi 1949, *Nephrotus* Meyer 1851, *Omphalodus* Meyer 1847, *Oxypteriscus* Matveeva 1958, *Pasambaya* Rusconi 1946, *Schigospondylus* Frič & Bayer 1902.

V. SUMMARY

This paper is the second of a series intended to form the basis for a revision of the palaeoniscoid fauna of the British Carboniferous. The type species of three genera from this fauna are redescribed and for comparative purposes two other type species from the Upper Carboniferous of Czechoslovakia.

Eight new Palaeonisciform families are erected. They are the Osorioichthyidae which appears to be an independently derived side line from the ancestral stock; the Gonatodidae, a family close to the Acrolepididae and to the Amblypteridae; the Gyrolepidotidae allied to the Acrolepididae–Elonichthyidae complex; the Atherstoniidae, a family close to the Trissolepididae; the Lawniidae which was probably derived from the Gonatodidae; the Cosmolepididae, Brachydeymidae and the Boreosomidae. One other new chondrostean family is proposed, the Habroichthyidae which belongs to the Peltopleuriformes.

A new genus *Pseudogonatodus* is erected for *Gonatodus parvidens* Traquair (1892) and it is also used to include *Gonatodus macrolepis* Traquair (1877).

The classification and evolution of the Palaeonisciformes is discussed and since all the chondrostean orders stemmed from the Palaeonisciformes, the subsequent evolution of the Subclass Chondrostei is outlined and a complete classification of the Subclass is attempted.

VI. ACKNOWLEDGMENTS

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VII. LETTERING USED IN TEXT FIGURES

Ang	angular	mp	median pit line
Ant	antorbital	Mx	maxilla
ap	anterior pit line		
Art	articular	Na	nasal
		na_1	anterior nasal aperture (nostril)
Br	branchiostegal ray	na_2	posterior nasal aperture (nostril)
can.W	canals of Williamson	o	pore
Cl	cleithrum	Op	opercular
Clav	clavicle	orp	postmaxillary sensory line
Cor	coronoid		
c.sp	cell spaces	Pa	parietal
		Pop	preopercular
d	dentine	pp	posterior pit line
Den	dentary	Ptr	postrostral
Dpt	dermopterotic		
Dsp	dermosphenotic	r	ridges of enamel
d.t	dential tubules	r.can	radial canal
Dyh	dermohyal	r.cr.con	radial cross connection
		R.pmx	rostro-premaxillary
e	enamel	R.pmx.ant	rostro-premaxillo-antorbital
Exsc	extrascapular		
		Sbo	suborbital
fe	fenestra	Scl	supracleithrum
Fr	frontal	sc.r.	sclerotic ring
		Sh.f	Sharpey's fibres
Gu	gular plate	So	supraorbital
		soc	supraorbital sensory canal
hc	supramaxillary sensory line	Sop	subopercular
h.la	horizontal bone lamellae	Ssc	suprascapular
h.v.can	horizontal network of canals		
Hy	hyomandibular	B.M.N.H.	British Museum (Natural History), London
Inf	infraorbital	R.S.M.	Royal Scottish Museum, Edinburgh
infc	infraorbital sensory canal		

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PLATE 1

Sphaerolepis kounoviensis Frič.

Photograph of cast of one of the syntypes. × 2·8.

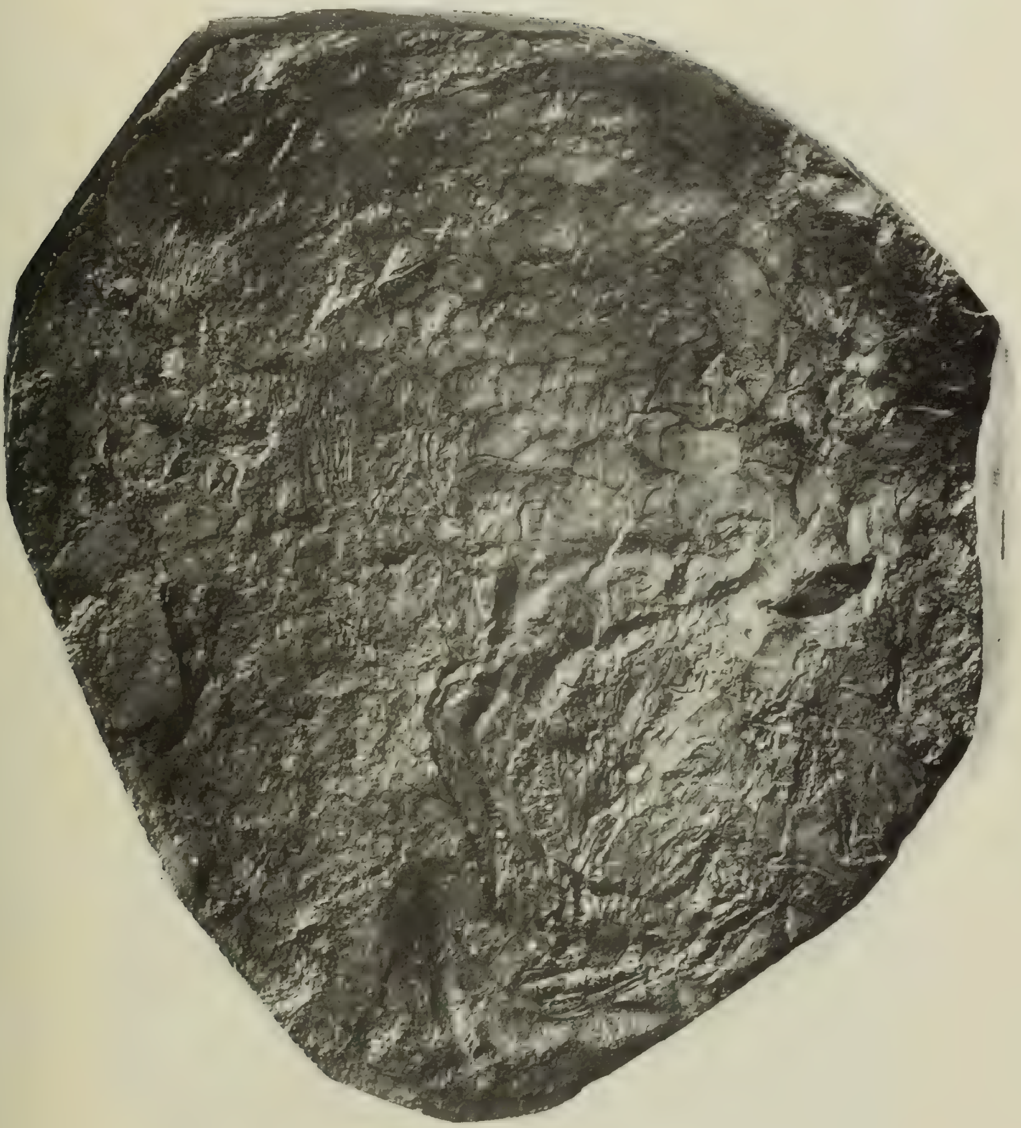


PLATE 2

Sceletophorus biserialis Frič.

Photograph of cast of one of the syntypes. ×3·5.

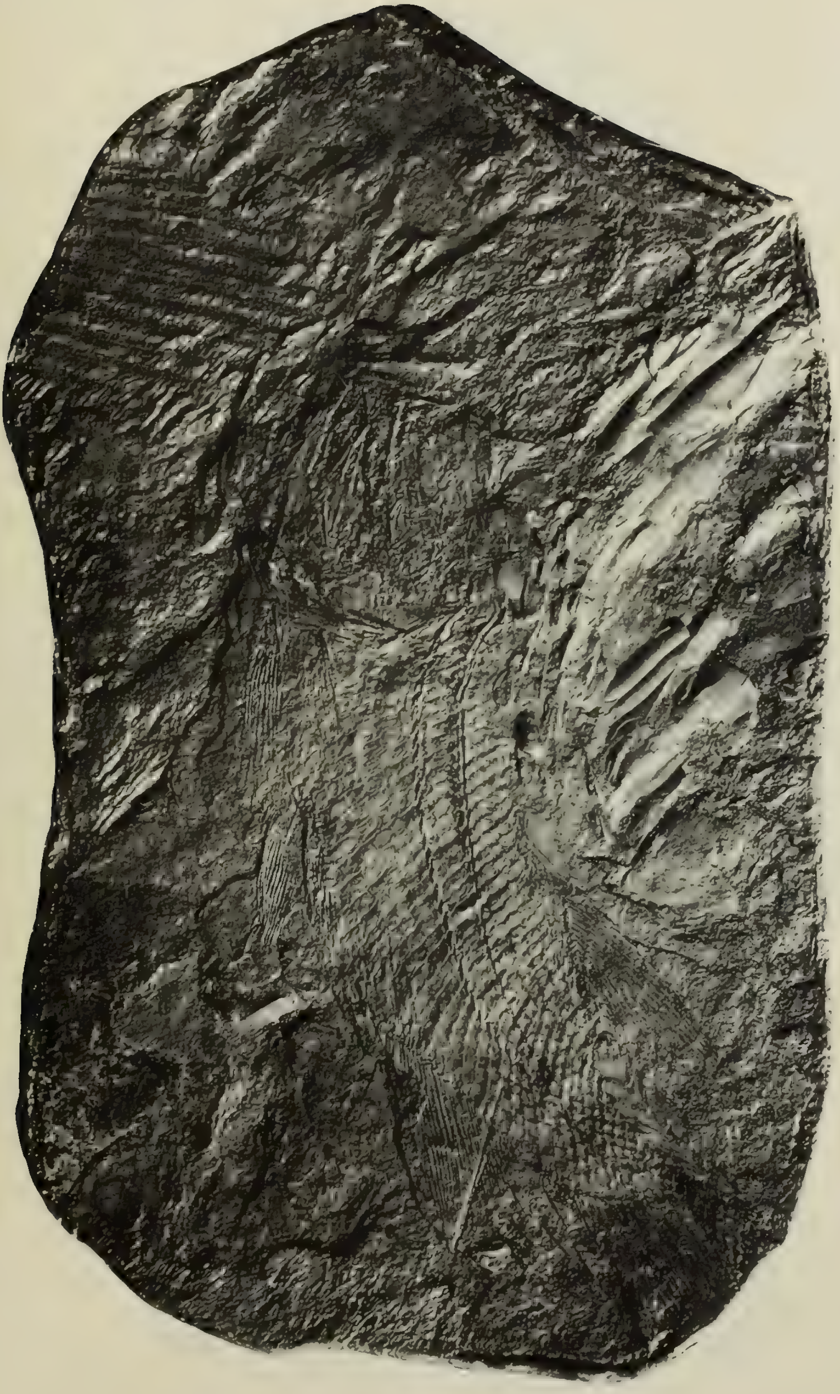
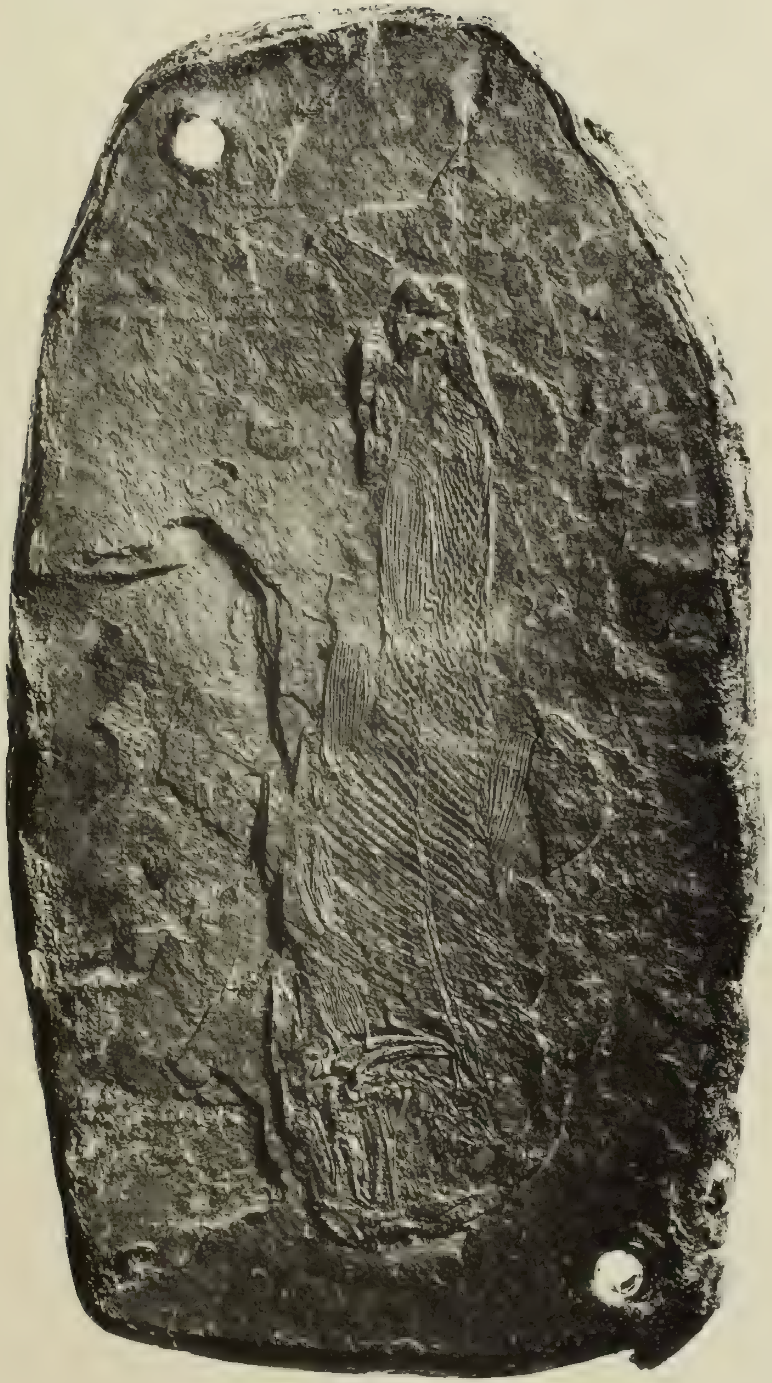


PLATE 3

Sceletophorus biserialis Frič.

Photograph of cast of one of the syntypes. × 3·1.



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BY

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LOWER CARBONIFEROUS TRILOBITES OF NORTH DEVON AND RELATED SPECIES FROM NORTHERN ENGLAND

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SYNOPSIS

A systematic description is given of the known Carboniferous trilobites from Devon. *Phillipsia leei, Phillibole coddonensis* and *Spatulina spatulata,* originally described by Woodward, are redescribed, together with *Phillibole polleni* and *Diacorphye ? vandergrachtii* from northern England. *Macrobole* cf. *brevispina, M.* cf. *laticampa, Phillibole aprathensis* and *Liobole glabra* previously described from Poland and Germany, are recognized among the specimens from Devon and described. *Phillibole culmica* from Germany is identified with *P. coddonensis.* Three new species, *Waribole chudleighensis, Spatulina longispina* and *Typhloproetus cephalispina,* are described.

Five successive trilobite faunas are tentatively recognized in the Devon Carboniferous, and their ages relative to the goniatite time-scale discussed. They are characterized by (i) *Macrobole* aff. *laticampa* (low zone II), (ii) *Spatulina* (II–IIIα), (iii) *Phillibole coddonensis* (IIIα) (iv) *P. aprathensis* (IIIα) and (v) *Phillipsia leei* (IIIβ–IIIγ).

I INTRODUCTION

THE Carboniferous trilobites of the British Isles can be divided into two groups, whose distribution appears to be closely linked with lithological facies. On the one hand are the large, robust, thick-shelled and heavily ornamented species, often with large eyes, which are found in the limestones of " reef " and " massif " facies of the Carboniferous limestone. On the other hand, in the radiolarian cherts and shales which characterize the Lower Carboniferous of south-west England is found a different group, which occasionally penetrated northwards in a shale facies to northern England. This latter group comprises generally small forms, their tests thin and fragile, mostly smooth, and their eyes small or absent. It is reasonable to assume that these represent a hemi-pelagic fauna of the open sea, whilst the former group is part of a shallow water benthos. This account sets out to describe the hemi-pelagic group in detail, and to examine their stratigraphical distribution. In contrast to the " limestone " fauna, which is dominated by the Family Phillipsiidae, the trilobites of south-west England consist largely of members of the Cyrtosymbolinae; the latter sub-family, however, is by no means confined to this facies, and includes many robust and large eyed forms of both Devonian and Carboniferous age.

A reappraisal of the classification of some of these trilobites has been made by Hahn (1965). In his scheme the following species described herein would be classified as follows:

Cyrtosymbole (*Macrobole*) aff. *laticampa* = ? *Carbonocoryphe*
Cyrtosymbole (*Macrobole*) cf. *brevispina* = *Archegonus* (*Phillibole*) *brevispina* group
Cyrtosymbole (*Waribole*) *chudleighensis* = *Archegonus* (*Waribole*)
Phillibole aprathensis
Phillibole polleni } = *Archegonus* (*Phillibole*) *aprathensis* group.
Phillibole coddonensis

The first detailed descriptions of these trilobites were by Woodward (1884), who erected three new species of *Phillipsia* in an appendix to his monograph of Carboniferous trilobites, thus tacitly commenting upon their separateness. The collections from the radiolarian cherts of Devon by Hinde & Fox (1895) enabled Woodward to indicate the presence of several new forms, and later (1902), using the more extensive collections of the local amateurs J. G. Hamling and A. Coomáráswamy, he was able to give more complete descriptions of these species. In 1909 I. Thomas described comparable faunas from South Devon, but since that time little attention has been paid to these fossils in this country. In the course of major revisions of Upper Palaeozoic trilobites in Germany, R. & E. Richter (1937–1951) described many new genera and species, making comparisons with the specimens described by Woodward. Similar work has been carried out in Czechoslovakia by Přibyl (1950) and Chlupac (1961), and in Poland by Osmólska (1962). The stratigraphical revision of the North Devon succession by J. M. Thomas, E. E. Swarbrick and the writer has established the horizons of the described trilobites more firmly, and has added much new material (see p. 238). In the course of similar studies in the underlying Pilton Beds, Goldring (1955) has drawn stratigraphical conclusions from the comparative work of Richter. The northern representatives of this fauna were described first by Woodward (1894), but since then they have been mentioned only briefly in stratigraphical descriptions in Geological Survey Memoirs (e.g. Calver & Ramsbottom 1962).

When preserved in chert, or in cherty shale, the test of these trilobites is commonly replaced by finely crystalline silica; in consequence the outer lamina of the test adheres firmly to the external mould, and the inner lamina to the internal mould. Thus the external view of the outer lamina is rarely seen. In contrast, specimens preserved in shales are found either as normal internal or external moulds, or with their dorsal exterior exposed. Thus the mode of preservation can fundamentally alter the appearance of the fossil, and this has given rise to much confusion in the past. Thus the " brim " of the cephalon or pygidium as described by Woodward often proves to be the mould of the ventral doublure. Moreover, there are sometimes structural differences between the outer and inner lamina. In *Phillibole polleni* for example, the outer surface of the glabella is smooth and unfurrowed, while the inner lamina bears strong furrows ; in *Phillipsia leei* the interpleural furrow sof the pygidium are visible on the internal but not on the external lamina. Thus the greatest care is necessary in the examination and description of this material, and comparison with earlier descriptions is by no means easy.

II SYSTEMATIC DESCRIPTIONS

Conventions and abbreviations

The conventions adopted in the systematic descriptions are those used in the Treatise of Invertebrate Palaeontology (Harrington *in* Moore 1959). For description of facial sutures the α–β–γ–δ–ϵ–ω system is adopted from R. & E. Richter (1949 : 68). Lateral glabellar lobes and furrows are numbered from posterior to anterior, 1p being the first anterior to the occipital furrow. The directions sagittal (abbreviated *sag.*), exsagittal (abbreviated *exsag.*) and transversal (abbreviated *tr.*) are indicated where doubt exists of the meaning of width (*W.*) or length (*L.*).

Described material is deposited in museum collections ; these are indicated by the following abbreviations.

BMNH—British Museum (Natural History)
GSM—Geological Survey & Museum
NDA—North Devon Athenaeum, Barnstaple
KCL—King's College, London

Family **PHILLIPSIIDAE** Oehlert 1886 emend. Hupé 1953

Genus ***PHILLIPSIA*** Portlock 1843 emend. Weller 1936

Type species. *Phillipsia kellii* Portlock by subsequent designation, Vogdes 1890.

Phillipsia leei Woodward

(Pl. 1, figs. 1–6 ; Text-fig. 1)

1884 *Phillipsia leei* Woodward : 66–68, pl. 10, figs. 1–4.
1884 *Phillipsia minor* Woodward : 68, pl. 10, figs. 5, 6*a*, *b*, 7, 8*a*.
1884 *Phillipsia cliffordi* Woodward : 69, pl. 10, figs. 8*b*, 9–12.
1884 *Phillipsia articulosa* Woodward : 70, pl. 10, figs. 6*c*, *d*, 13.
1909 *Phillipsia minor* Woodward ; Thomas : 201, pl. 7, fig. 11.
1909 *Phillipsia* cf. *minor* Woodward ; Thomas : 201–2, pl. 8, figs. 12, 13.
1909 *Phillipsia* sp., Thomas : 202, pl. 7, fig. 14.

Diagnosis. Small *Phillipsia* with internal punctation but no external granulation to carapace ; glabellar furrows other than 1p very indistinct or absent ; pygidium with clearly defined border ; pygidial and cephalic borders with longitudinal striations on underside.

MATERIAL. The specimens upon which Woodward based his original description was obtained from Waddon Barton Lane, near Chudleigh, Devon by Mr. J. E. Lee. Some of these were presented by Woodward to the British Museum (Natural History) at the time, while others remained in Lee's private collection at Torquay. On Lee's death, his collection was transferred to the British Museum.

Specimen BMNH. In. 58281, figured by Woodward (1884, pl. 10, fig. 2) is here selected as lectotype ; this is one of the few specimens which displays an external view of the external shell-lamina, and includes some attached thoracic segments (Pl. 1, fig. 1). Specimen BMNH. In. 5280, one of the syntypes figured by Woodward (pl. 10, fig. 3) shows additional cephalic features and the internal view of the outer shell-lamina is here illustrated (Pl. 1, fig. 2). Specimen BMNH. In. 58283, figured as *P. cliffordi* by Woodward (1884, pl. 10, fig. 10), here considered to be a synonym of *P. leei*, shows the pygidial characters of the species. *P. articulosa* BMNH. I. 1861 (Woodward, pl. 10, fig. 13) and *P. minor* BMNH. I. 1860 (Woodward, pl. 10, fig. 7*c*) are also considered to be synonyms of *P. leei*. The Waddon Barton material contains, in addition to the type specimens, 6 nearly complete cephala, 7 cranidia, 6 free cheeks, 10 fragments of thorax, and 46 pygidia. In addition two specimens from Waddon Barton are in the Museum of the Geological Survey, where also, those figured by I. Thomas (1909) are preserved. Additional material from North Devon, has been collected by the author and by J. M. Thomas and is preserved at King's College. A further 10 specimens have been found by M. R. House in excavations in Ugbrooke Park, Chudleigh. A single headshield was collected from a comparable horizon in the north-east Rhenish Schiefergebirge by G. Warrington.

HORIZON AND LOCALITIES.

1. Red-stained black cherty shales, associated with *Neoglyphioceras spirale* and *Mesoglyphioceras* aff. *granosus* i.e. P_{1a}—P_2 (Butcher & Hodson 1960) at Waddon Barton Lane, Chudleigh, Devon, in sides of lane leading south from Waddon, one mile east of Chudleigh. Nat. Grid Ref. SX 885793. Also similar shales in various trenches in and around Ugbrooke Park, Chudleigh.
2. White chert : Horizon unknown at Hestow Farm, Ideford, Devon. One mile due south of Ideford, near Chudleigh, Devon. Nat. Grid Ref. SX 888761.
3. Upper Shales and limestones associated with *N. spirale* at Whipcott Quarry, Westleigh, N. Devon. Nat. Grid Ref. ST 075188 (J. M. Thomas collection).
4. Upper Shales and limestones, associated with *Posidonia becheri*. Hole Lake Farm Quarry, Staple Cross, Huntsham, N. Devon. Nat. Grid Ref. ST 022208 (J. M. Thomas collection).
5. Rhenaer Kalk (Bed 23, Meischner 1962) associated with *G. spirale*. Aartalstrasse Adorf-Flechtdorf, north-east Rhenish Schiefergebirge.

DESCRIPTION. Cephalon. Outline nearly semicircular, slightly shorter (sag.) than width (tr.) ; posterior border almost straight. Glabella does not reach anterior margin : outline rounded anteriorly, almost parallel sided but slightly constricted medianly ; maximum width less than half length. Anterior of glabella high and globose, lower posteriorly. Occipital segment of glabella clearly demarcated by deep occipital furrow which is slightly bent forward centrally ; smoothly rounded, narrow (sag.). 1p furrows very deep, backwardly directed to join occipital furrow at points 1/3 along its length ; cut off high triangular glabellar lobes. 2p furrows very faint or absent. Axial furrow sharp, separating glabella from almost flat fixed cheek. Glabella reaches forward to touch narrow, smooth, raised anterior rim. Facial suture cuts anterior margin at a point (α) immediately in line (exsag.) with the forward projection of the sides of glabella at its minimum width, swings outwards sharply to point β which lies in line (tr.) with the maximum width of the glabella, gently curves round to subparallel, slightly convergent with axial furrow to eye region, which lies in line or immediately posterior of 1p furrows. From posterior of eye (i.e. immediately in front of occipital furrow) swings sharply outwards to cut posterior margin of headshield (ω) a short distance inside angle of genal spine. Thus fixed cheek has sharply pointed triangular extension in occipital region. Eye moderately small, less than $\frac{1}{4}$ length of headshield, reniform, multilensed, situated on a raised platform surrounded by a shallow depression. Free cheek gently inflated, with shallow border furrow and deep pleuroccipital furrow meeting at high angle in genal region. Brim flattened with rounded external margin ; on underside carries fine subparallel longitudinal striae, six or seven laterally, diminishing to 4

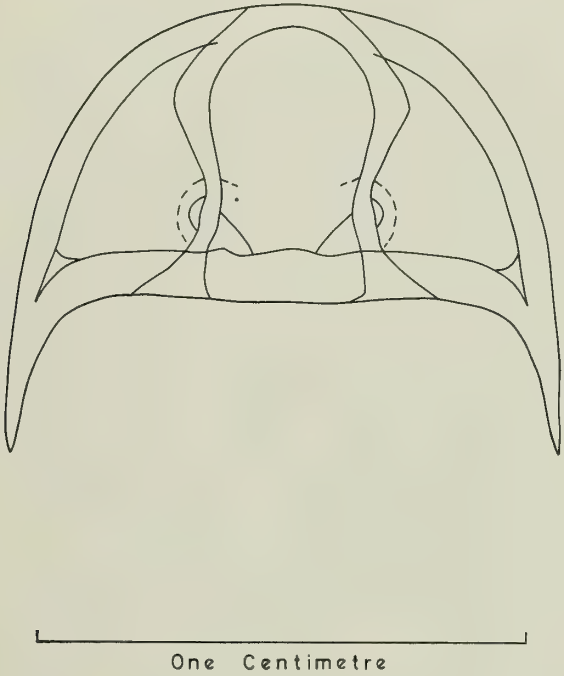


FIG. 1. *Phillipsia leei* Woodward. Reconstruction.

anteriorly: 3 or 4 striae continuous with striae on underside of pre-glabellar brim and of genal spine. Spine in direct continuity with cephalic brim; broadly based tapering evenly to a sharp point; length variable from less than half to nearly equal to sagittal length of cephalon; striae on underside externally continuous with those on cephalic brim; inner striae bend sharply round at genal angle to parallel occipital margin. Whole of interior of cephalon except brim ornamented with a fine indistinct punctation, showing no definite arrangement on cheeks, but a vague alignment into transverse rows on the underside of the glabella. Hypostome has spatulate outline, with strongly elevated median body and flat wings: anterior border convex forward, antero-lateral angles a little more than 90°; posterior border a smoothly rounded parabola. Median body high, subrectangular outline, touches anterior border.

Thorax. Consists of 9 segments: axis clearly defined, distinctly higher than pleural region; axis approximately 1/3 width (tr.) of thorax. Axial rings with raised posterior border, sloping forward to a deep straight transverse furrow which divides it from articulating half-ring, which is narrow (sag.) and triangular with a strong rounded ridge anteriorly. Pleural regions moderately flat, pleural segments nearly straight with a broad triangular articulating flange at anterior and distinct posterior ridge. Pleural grooves strong and deep, subcentral, slightly oblique. Pleural extremity truncated, with a short backwardly directed spine.

Pygidium. Outline hemielliptical, somewhat wider (tr.) than long (sag.). Anterior margin nearly straight, inflected forward into a broad triangular flange in the pleural region, deflected slightly forwards in axial region; antero-lateral angles smoothly rounded. Axis 1/3 or more of width (tr.) anteriorly, tapering rapidly to a smoothly blunt extremity in contact with posterior brim. Axial rings 10 to 14, separated by straight furrows which are quite distinct except at extreme posterior. Axial furrow distinct. Pleural regions flatly arched, with 8–10 clear pleural grooves; anterior groove is nearly parallel with anterior margin, posterior grooves become increasingly oblique. Pleural ridges strongly asymmetrical, with steep slope facing backwards. Pleural grooves become somewhat fainter posteriorly, but are never effaced; each groove ends abruptly at the pygidial brim. Interpleural furrows sometimes visible as a faint ridge on the underside of the pygidium, at most over whole length (tr.) of pleural segment anteriorly, but mostly only at extremities of first two or three segments; at the brim they are sharply deflected backwards. On the internal mould these interpleural furrows make the pleural grooves seem bifid. Pygidium with a narrow brim, without clearly defined furrow on dorsal side. Ventral doublure on underside flat, narrow anteriorly widening rapidly posteriorly, but without trace of mucronation. Underside of brim carries fine slightly irregular subparallel longitudinal striae, 4 or 5 external striae continuous around pygidium; additional striae, up to 9 in all, inserted at inner side as brim broadens to posterior. Whole underside of pygidium except brim finely punctate. Axial rings have up to 10 moderately large widely spaced punctae along their posterior margins; in the posterior rings these punctae are anterioposteriorly elongate and occupy the whole axial ring length (sag.). In each pleural segment there are three transverse rows of punctae; the coarsest are immediately anterior of the intersegmental boundary, the other two rows are finer, none occurring anterior of the pleural groove. The punctae are fainter in more posterior segments. Appendage muscle scars strongly developed on one specimen (BMNH. In. 55935, Pl. 1, fig. 7) as shallow circular depressions on sides of front five axial rings.

DIMENSIONS (in mm.)

	Cephalon		Pygidium		Axis
BMNH	L. (sag.)	W. (tr.)	L. (sag.)	W. (tr. ant.)	W. axis (tr. ant.)
In. 58281	6·0	11·2			
I. 864	2·4	4·8			
I. 1064		4·5			
I. 1090			5·0	5·5	1·8
I. 1092	5·0				
In. 55902			4·8	3·0	
In. 55903			4·8	7·2	2·1
In. 55914				9·0	3·9
In. 55917			4·0	7·2	2·5
In. 55919			5·3	12·4	3·2
In. 55932	10·3	16·4	9·0	12·5	
In. 55935			8·9	9·9	
In. 55938			4·9	6·0	
GSM					
23434			4·0	4·0	

REMARKS. Woodward (1884) identified four species from among the Waddon Barton material. In view of the continuity of variation displayed by this assemblage, however, I would regard them as constituting one species. *Phillipsia cliffordi* was distinguished solely on pygidial characters. Woodward appears to have been misled by the different aspects afforded by the internal moulds, and to have given the name *cliffordi* to those moulds which show an apparently broader brim, and in which the traces of the intersegmental boundary give the appearance of bifurcation to the pleural grooves. *P. minor* appears to have been distinguished by the characters of the head-shield, but the differences were not specified. The curvature of the genal spine in pl. 10, fig. 6*a* is, as is apparent from the counterpart (BMNH. I. 1864), due to the superimposition of a thoracic segment upon the genal angle. The original of pl. 10, fig. 7*c* (BMNH. I. 1860) shows that this same feature is a misrepresentation. *P. articulosa* was described as having 17 coalesced segments in the pygidial axis. No specimens in the Lee collection have this number, and indeed the two specimens in figure 6, whose counterpart has been preserved, show the normal 12–13 (as in fact Woodward's figure shows) while the original of figure 13 (BMNH. I. 1861) shows that 3 thoracic segments have been drawn by the artist as part of the pygidium.

I. Thomas (1909) followed Woodward's definitions but suggested that one of his own specimens might be separable as it possesses a strong second pair of glabellar furrows. Examination of the specimen (GSM. 23436) leaves no doubt that these furrows were produced by the crushing of the carapace into the first pair of furrows.

The generic and family affiliations of this species are difficult to determine. This is due partly to the different definitions of the possible groups given by various authors. It would fit within the family Phillipsiidae as defined in the Treatise of Invertebrate Palaeontology (Weller *in* Moore 1959 : 399) except for the absence of more than one pair of glabellar furrows. However, this feature is not regarded as diagnostic by Hupé (1953) whose description in an amended form is purported to have been used in the " Treatise ". Alternatively Hupé does insist that a granular test is characteristic of the family, which the " Treatise " definition does not make essential. Despite these minor points, however, the form of the glabella, the relatively narrow pre-glabellar region, and the multisegmented pygidium, place the species clearly in this family.

The species fits the definitions of the genus *Phillipsia* as emended by Weller (1936 : 704 ; 1959 : 399) except in having a well defined border or flange to the pygidium. In fact, the holotype of *Phillipsia kellii* Portlock 1843 (GSM. 63045) the type species of *Phillipsia* by subsequent designation, does have a quite clearly defined, though narrow, pygidial border. It does, however, possess 3 clearly defined glabellar furrows and a very well-marked surface granulation. Since neither of these characteristics is regarded by Weller (1936, 1959) as diagnostic of the genus, the most satisfactory course seems to be to retain the species *leei* in the genus *Phillipsia*. The present species differs in many ways from the very closely defined generic diagnosis of Reed (1942*b*), who based his definition upon *Asaphus gemmuliferus* of Phillips. Reed's emendation is framed in such detail as to exclude all but the type species and I prefer to follow the less rigidly defined diagnosis of Weller (1959). The two genera *Paladin* Weller 1936 and *Kaskia* Weller 1936 possess similarities to the present species, and have a more clearly defined pygidial border than *Phillipsia kellii*, but both have very large eyes occupying a large area of the free cheek, are strongly granulose externally and have an anterior expansion of the glabella. The species has some characters in common with *Weberides* Reed 1942*b*, notably in the internally striated border to the cephalon and pygidium ; but again the small size of the eyes, and the absence of anterior glabella expansion exclude it from this genus.

Family **PROETIDAE** Salter 1864

Subfamily **CYRTOSYMBOLINAE** Hupé 1953

Genus ***CYRTOSYMBOLE*** R. Richter 1913

Subgenus ***MACROBOLE*** R. & E. Richter 1951

TYPE SPECIES. *Cyrtosymbole* (*Macrobole*) *drewerensis* R. & E. Richter 1951. *Macrobole*, first proposed by R. & E. Richter (1951), has subsequently been given a fuller diagnosis (*in* Moore 1959). Many species of this genus have been described from Germany, Poland and Czechoslovakia, but it is difficult to refer the few specimens from Devon to any of those species which in any case are not mutually comparable.

In view of the paucity of material it has been thought best not to erect new species, but to describe briefly individual specimens and note their affiliations.

The majority of the species belonging to this subgenus are found in Zone I of the Carboniferous, although some range into Zone II. Only if *Phillibole culmica* R. & E. Richter is accepted as a *Macrobole* could the subgenus be said to range into Zone III (see p. 238). In fact it is not easy to draw a line between *Phillibole* and *Macrobole* on cephalic characters, the former seemingly having evolved from the latter : but the strongly segmented tail of *Macrobole* contrasts markedly with that of *Phillibole*.

***Cytosymbole* (*Macrobole*) cf. *brevispina* Osmólska**

Pl. 2, figs. 1, 2.

1960 *Cyrtosymbole* (*Waribole*) cf. *aequalis* (Meyer) ; Prentice : 271, pl. 12, fig. 5.
1962 *Cyrtosymbole* (*Macrobole*) cf. *brevispina* Osmólska : 146, pl. 13, fig. 1.

DIAGNOSIS. *Macrobole* with clearly segmented glabella, moderately wide (long.) preglabellar field, pointed anterior margin to cranidium, short pointed genal spine.

MATERIAL. The specimen (KCL t182) previously figured by me (Prentice 1960) is presumed to have come from Bed X (see p. 238) at Park Gate Quarry, Tawstock, and consists of a crushed cranidium. Another cranidium from the same quarry (BMNH. I. 3223) contains on the same surface a free cheek presumed to belong to the same individual, together with two free cheeks and a pygidium of *Spatulina spatulata*.

HORIZON. Osmólska's specimens came from the upper beds of the *Pericyclus* Zone (i.e. the German zone II) ; while the Tawstock horizon has been correlated by the writer with the boundary of zones II and III α.

REMARKS. The broad-based, tapering glabella, with clearly defined occipital furrow and distinct backwardly directed 1p, 2p and 3p glabellar furrows are features which place the North Devon specimens clearly in the *Macrobole* group. The facial suture, expanded widely in front, lying close and parallel to the axial furrow in the palpebral region, and then extending rapidly outwards posteriorly, is also characteristic of the genus. The genera *Waribole* and *Archegonus* (to which the species *aequalis* is now referred) have facial sutures which diverge less abruptly from the axial furrow anteriorly and posteriorly, the eyes and palpebral lobes of *Waribole* are much larger, and the occipital lobe of the glabella is not of equal width throughout. Osmólska noted the presence of an anterior point to the cranidium in larval specimens of *M. brevispina*, but this is not evident in specimens of comparable size to the Devon examples. She does, however, refer to 7 cranidia as " cf. *brevispina* " which attain the length of 2 mm. without losing the anterior spine. The Devon specimens resemble these in their wide preglabellar field, and broadly rounded glabella front.

Cytosymbole* (*Macrobole*) aff. *laticampa Osmolska

Pl. 2, figs. 3, 5.

1962 *Cyrtosymbole* (*Macrobole*) *laticampa* Osmólska : 139, pl. 11, figs. 1–5.
1962 *Cyrtosymbole* (*Macrobole*) ? *laticampa* Osmólska : 141, pl. 11, fig. 7.

REMARKS : The specimens found in Devon consist of one cranidium preserved as an internal mould with the internal layer attached (Pl. 2, fig. 3), and its counterpart an external mould with outer layer attached, together with a portion of a cephalon (Pl. 2, fig. 5) which doubtfully belongs to the same species. The cranidium closely resembles *M. laticampa*, especially in having a wide (sag.) preglabellar field ; but this field carries a broad, deep excavation across its anterior which is unknown in *M. laticampa*. The part cephalon is larger than the cranidium, but its deeply lobed glabella and occipital segment of equal width (sag.) place it in *Macrobole* ; it has however a short librigenal spine, whilst that of *M. laticampa* is long.

Both specimens were found in a thin bed of white chert in an old quarry in Claypit Coverts, West Buckland (SS 662291) associated with goniatites of " pericyclid " type. The horizon is estimated to be a few feet above the base of the Chert Formation. *M. laticampa* in Poland is restricted to the *Gattendorfia* Zone (i.e. German zone I), but there is no other evidence to suggest that the Chert Formation begins in this zone : an attribution to zone II is therefore the most likely for this horizon.

Genus **CYRTOSYMBOLE** R. Richter 1913

Subgenus ***WARIBOLE*** R. & E. Richter 1926

TYPE SPECIES. *Cyrtosymbole* (*Waribole*) *warsteinensis* R. & E. Richter 1926.

Cyrtosymbole* (*Waribole*) *chudleighensis sp. n.

Pl. 2, fig. 7.

DIAGNOSIS. Minute Cyrtosymboliinids with smooth inflated glabella and widely diverging anterior branches to facial sutures.

HOLOTYPE and MATERIAL. The species is known from one block of specimens only, M. R. House collection 1100, BMNH. It. 1433, from Pit L (of House & Butcher 1962), at the eastern end of the field immediately north-east of Mount Pleasant, Chudleigh, Devon. The block contains abundant fragments of *Posidonia*, and is assigned to the " P " shales of the succession. Four cranidia, with attached and detached thoracic segments, 3 fragments of free cheeks and one pygidium are present all lying within 1 sq. cm. The cranidium figured in Pl. 2, fig. 7*a* is taken as holotype. The two larger free cheeks probably belong to *Phillipsia leei* (see p. 211) which also occurs at this horizon.

DESCRIPTION. Cephalon. Very small size, length (sag.) 1·3, 1·4 and 1·6 mm. Glabella strongly inflated, parallel-sided, with a steep, rounded, blunt anterior extremity. Occipital furrow distinct, strongly curved forward in centre, so that occipital segment is much wider (sag.) in centre than at sides. Occipital segment same width (tr.) as glabella. Anterior of glabella smoothly rounded and without furrows, 1p furrows shallow, extend diagonally from sides of glabella to join occipital furrow, thus cutting off small triangular lobe. Pre-glabellar field strongly concave, with narrow but distinct enrolled anterior rim. Facial suture cuts anterior border at some distance from the mid-point, then takes an almost semicircular course laterally and posteriorly, swinging inwards to the anterior of palpebral lobe (γ) at a point half way along length (exsag.) of glabella, and close to the axial furrow. From the posterior of the palpebral lobe (ϵ) the suture swings outwards almost parallel with the posterior margin of the cephalon ; i.e. almost along occipital furrow ; then gently back to cut posterior margin at a shallow angle distally. Fixed cheek is thus broad and elliptical in front, very narrow in palpebral region, and produced to a long point occipitally. The concavity of the preglabeller field extends on to the anterior of the fixed cheek, which rises along the sides of the glabella. Palpebral lobe high, crescentic, with two distinct palpebral ridges extending from inner side on to the rising flanks of the glabella immediately in front of the 1p furrow. Free cheek with strong marginal concavity and thin narrow rim. Genal angle probably with short spine.

Thorax. Number of segments unknown. Each segment has high arched axis, slightly less than $\frac{1}{3}$ of the total width of the thorax. Axial furrow deep. Axial ring has deep transverse furrow and an anterior ridge ; articulating half-ring narrow (sag.). Pleural regions shallowly arched, pleural furrows broad and deep. Pleural extremities obscure, perhaps truncate.

Pygidium. Short and subquadrate. Anterior margin strongly curved, with rounded lateral angles. Posterior margin a flattened curve, with a broad concave brim which reduces in width rapidly laterally and anteriorly. Axis short, conical, sharply tapering, with seven axial rings, each with a deep axial furrow. Pleural furrows six, deep and distinct, asymmetrical with steeper slope facing anterior. Anterior furrows reach margin, posterior ones become diagonal and are effaced laterally. Four most anterior interpleural furrows clearly defined.

Discussion. The generic affiliation of this species is problematical. It belongs with the Cyrtosymbolinae rather than the Phillipsiidae because of the presence of a pre-glabellar field, and the small number of segments in the pygidium. It is tentatively placed with the subgenus *Waribole* because it resembles the type-species *W. warsteinensis* in the following features : the possession of a strongly diagonal pair of 1p glabellar furrows, the position of the palpebral lobes, the lateral narrowing of the occipital ring, the short pygidial axis with few segments, and the broad pygidial border. If differs from this species mainly in having a parallel-sided glabella, and in the strongly diverging anterior branches of the suture line. In this latter feature it resembles *Carbonocoryphe* R. & E. Richter, the cranidium figured by R. & E. Richter (1950, pl. 1, fig. 12) as *Carbonocoryphe? ferruginia* showing a somewhat similar wide fixed cheek ; but the pygidial characters of this genus are quite unlike this species. A cranidium described under the name of *Cyrotsymbole librovitchi* var. *latilimbata* by Weber (1937 : 30, text-fig. 15) is very similar, but the associated pygidium has no widened posterior border ; that of *Cyrtosymbole librovitchi* var.

euryaxis (Weber 1937 : 30, text-fig. 14) has the same shape as the present species, but the axis does not taper so strongly. *Phillipsia krasnopolskii* Weber 1937 has some similarities, notably in the brim of the pygidium and the shape of the glabella, but has no pre-glabellar field and 10–11 axial segments in the pygidium.

Genus ***PHILLIBOLE*** R. & E. Richter 1937 : 108

Phillibole aprathensis R. & E. Richter

Pl. 7, figs. 6–9.

1882 *Phillipsia aequalis* Meyer; Kayser: 68, pl. 3, figs. 7, 8.
1882 *Phillipsia* aff. *Eichwaldi* Fischer ; Kayser : 73, pl. 3, fig. 6.
1895 *Phillipsia cliffordi* Woodward ; Woodward : 646, pl. 28, fig. 3*a* only.
1902 *Phillipsia polleni* (?) Woodward : 482, pl. 20, fig. 2, 13 only.
1932 *Cylindraspis aprathensis* R. & E. Richter ; Haubold : 216, 220, 223, 240 (nomen nudum).
1932 *Cylindraspis aprathensis* R. & E. Richter ; Kobold : 484, 508, (nomen nudum).
1937 *Phillibole aprathensis* R. & E. Richter : 109, text-figs. 1, 2.

DIAGNOSIS. *Phillibole* with rounded triangulate headshield : tapering glabella with slight but distinct median constriction ; long, distinctly segmented pygidium with long tapering axis reaching nearly to posterior extremity.

MATERIAL. Two cranidia (BMNH. In. 228912, In. 18415) and one pygidium (BMNH In. 18420) from Coddon Hill (SS 5729): cranidia (BMNH. I. 4559, NDA. 807 (Woodward 1902, fig. 13), and NDA 808), free cheek (BMNH. I. 4563) and pygidium (BMNH. In. 18413) from Hannaford Quarry (SS 6029); free cheek (KCL t174) from Templeton Quarry, Tawstock (SS 542297) ; cranidium and counterpart from a loose block above Warrenshill Copse, Bampton (SS 978222) (BMNH It. 1434 *a*, *b*) ; pygidium from Upper half of Chert Beds, Trench Q, Ugbrooke Park, (House coll. 429) ; cranidium and part of thorax (BMNH. I. 1435) Kersdown Beds, Little Holwell Quarry, Bampton (SS 964232).

HORIZON. The holotype is from the Posidonien-schiefer (horizon IIIβ) of Aprath (R. & E. Richter 1937). Haubold (1932) records the species in association with *Goniatites intermedius* (IIIα/β) and with *G. falcatus* and *G. waddingtoni* (IIIβ) ; he also records it doubtfully with a IIIγ_2 fauna. Kobold (1932) records the species from IIIγ_1 at Ecksberge in the Harz. However, the associated fauna includes goniatite species subsequently renamed *G. striatus mucronatus* and *G. striatus koboldi* (Pickel 1937 ; Ruprecht 1937), as well as *G. granosum spirale* ; a fauna which was attributed to the IIIβ_7 subzone by Pickel and which compares closely with that of P_{1d} in the British Isles (cf. Hudson & Cotton 1945 : 275). A range from the top of IIIα (= upper P_{1a}) to the base of IIIγ (=P_{1d}—P_{2a}) is thus indicated for this species. This lies within the known stratigraphical range of the Chert Formation in Devon, from which all the specimens are derived. *Ph. aprathensis* has not been found in close association with *Ph. coddonensis* and there is a little evidence to suggest that it may occupy a higher stratigraphical horizon than the latter.

DESCRIPTION OF DEVONSHIRE MATERIAL. Glabella long, with broad base, evenly attenuated with slight median constriction ; anterior rounded slightly pointed.

Anterior of glabella higher than posterior. Occipital segment wide (sag.), slightly wider at sides than in centre ; occipital furrow almost straight, distinct. Trace of occipital spine or pustule on centre of occipital segment. Glabellar furrows faint ; 1p curved backwards to cross occipital furrow at less than a third the transverse distance from the sides, then projected straight back across the occipital segment to the posterior margin ; 2p strongly bent back to join 1p, 3p slightly less strongly curved backwards. Axial furrow clear and deep. Preglabellar field narrow and concave, rising gently to an enrolled brim. Fixed cheeks rise from the anterior concavity along sides of glabella, flat behind. Facial suture begins (α) within the projection forward of the axial furrow at the mid-point (exsag.) of the glabella, swings sharply outwards to β, which is rounded and lies behind the line of the glabella anterior; then swings back inwards and from midline of glabella length lies parallel and close to the axial furrow. After crossing the occipital furrow it swings sharply outwards to cut the posterior margin some distance from the axial furrow. Eye lobes very long and very slightly curved, almost impossible to distinguish.

Free cheek gently inflated, with shallow marginal concavity rising to an ill-defined narrow enrolled rim. Pleuroccipital furrow straight, poorly defined; pleuroccipital segment broad, gently inflated, of equal width throughout. Genal angle with small, short, sharply pointed spine. Eye surface comparatively large, inner margin nearly straight, outer margin strongly curved ; surface flat, finely but irregularly reticulate. Ventral doublure broad, curved, with four irregularly spaced parallel striae on the inside.

Thoracic segments with broad axis, clear axial furrow. Pleural sectors with strong median pleural furrow.

Pygidium parabolic in outline ; axis high and distinct, broad at anterior, nearly equal to one-third of the width of the pygidium, rapidly tapering to a moderately blunt extremity a little short of the posterior border. 7 to 10 axial rings, transverse furrows moderately distinct to end of axis. Traces of pygidial appendage muscle scars on the three anterior rings. Pleural regions gently arched, pleural furrows 4 to 6, becoming effaced posteriorly ; strongly oblique, terminating at edge of pleural field. Trace of interpleural furrows on two anterior segments. Border furrow moderately sharp, rim enrolled with roof-shaped cross-section ; faintly longitudinally striate. Post-axial field flat, no post-axial ridge.

REMARKS. *Phillibole aprathensis* is a larger trilobite than *Ph. coddenensis* ; it most nearly resembles *Ph. polleni*, from which it may be distinguished by the triangulate form of the headshield, the faint median constriction of the glabella, and the longer pygidial axis. A closely similar form described by Stubblefield (*in* Calver & Ramsbottom 1962) as *Phillobole* aff. *aprathensis* from B_2 horizons in the north of England, differs in having a slightly wider fixed cheek in the post-ocular region.

Phillibole polleni (Woodward)

Pl. 4, figs. 1–4.

1894 *Phillipsia polleni* Woodward : 487, pl. 14, figs. 7–12.
1962 *Phillibole polleni* (Woodward) Calver & Ramsbottom : 180.

DIAGNOSIS. *Phillibole* with nearly semicircular headshield; gently tapering glabella without median constriction. Pygidial axis with a blunt, rounded extremity which lies some distance in front of posterior border.

LECTOTYPE. BMNH It. 371*a* (figured Woodward, 1894, pl. 14, fig. 9) here selected as lectotype.

MATERIAL. The lectotype and all specimens figured by Woodward are preserved in the British Museum (Natural History), under registered numbers It. 369–374. All are preserved as slightly flattened carapaces in shale, with the original structure of the outer lamina preserved, or as external moulds of this. The structure of the inner lamina can be rendered visible through the test by wetting the surface.

LOCALITY AND HORIZON: The species is only known from the type locality; the banks of the River Hodder near Stonyhurst, Lancashire. According to Calver & Ramsbottom (1962 : 180) this horizon lies above the *B. hodderense* Beds, in beds equivalent in age to the Pendleside Limestone. The upper part of this limestone belongs to the B_2 zone, the lower probably to B_1, and *Phillibole* cf. *polleni* has been recorded in association with *Bollandoceras hodderense* (Calver & Ramsbottom 1962 : 311–312) at some Pendleside Limestone localities. It may thus be assumed that the stratigraphical horizon is at or just below the B_1/B_2 zonal boundary (see p. 238).

DESCRIPTION. Carapace moderately large, flatly arched, with a broad, rather prominent axis. Test moderately thin.

DIMENSIONS (in mm.):

	It. 371	It. 369	It. 370
L. cephalon . . .	9·5	—	7·8
W. cephalon . . .	16·0	—	10·8
L. glabella . . .	6·0	—	
L. pygidium . . .	7·8	5·1	6·2
W. pygidium . . .	14·0	9·8	12·0
W. pyg. axis . . .	6·0		

Cephalon nearly semicircular in outline. Glabella broad at base, tapering forward, front bluntly rounded with axial furrows straight or slightly convex. Occipital segment equal in length sagitally and exsagitally. Occipital furrow nearly straight but composed of three equal, forwardly convex, curves. Anterior of glabella smooth, lateral furrows not visible externally. Internally there are three short, backwardly directed furrows. 1p begins at axial furrow a greater distance in front of occipital segment than the length (sag.) of the latter; gently curved backwards at first then sharply inclined towards occipital furrow. 2p not so far in front, parallel with lateral part of 1p; short. 3p closer still, and shorter. Preglabellar field narrow, deeply concave rising to a high, strongly enrolled rim, which bears 3 or 4 subparallel longitudinal striations on its upper surface. Fixed cheeks flat along sides of glabella. Facial suture begins (α) in line with, or slightly wide of, the forward projection of the axial furrows at the base of the glabella; swings sharply outwards to β, so that α–β is very short; then back in a smooth outwardly convex curve to very near axial furrow at γ. γ–δ–ϵ is a smooth outwardly convex curve along side of glabella reaching nearest point to axial furrow just ahead of the pleuroccipital furrow. From here bends sharply outwards across pleuroccipital furrow to cut the posterior margin (ω) at internal angle of genal spine. Fixed cheeks thus widely expanded in front, narrow along sides of glabella, with palpebral lobe situated almost exactly half way along length of cranidium. Pleuroccipital furrow sharp. Posterior margin straight adaxially, laterally bent back into a posteriorly projecting curve.

Free cheeks broad, only slightly inflated, with a broad marginal concavity which rises laterally to a narrow, strongly enrolled rim ; this is broader anteriorly and narrower laterally and carries 3–4 parallel striations. Genal spine very short, sharply pointed ; outer edge in direct continuation of the cephalic curve ; inner edge concave so that posterior margin of the free cheek is deeply notched. Eye platform large, flat, kidney-shaped ; eye with numerous lenses, arranged in two intersecting series concentric upon the anterior point and a point on the inner margin one third eye-length from posterior. Ventral doublure broad, bearing two strong subcentral and several irregular lateral subparallel longitudinal striae, all of which continue on to genal spine. Pleuroccipital furrow clear, dying out laterally ; pleuroccipital segment slightly raised.

Thorax. Consists of 9 segments. Axis broad, considerably broader than pleural fields, gently arched. Axial furrows sharp. Axial ring equal width (sag. and exsag.) across axis ; a deep transverse groove is situated immediately under the posterior margin of the preceding ring ; from this the ring rises flatly to the posterior margin, which is sharply angulate and carries a row of small pustules.

Pleural fields arched a little less than the axis ; pleurae inflected dorsally and posteriorly at the mid-length. Pleural segments of equal width throughout, with a sharp posteriorly-directed point at their extremity. Pleural furrows moderately deep and broad, sub-central ; otherwise the surface of the pleurae are flat, inclined forward beneath the posterior of the preceding segment.

Pygidium. Anterior margin straight in centre, slightly bent back laterally from mid-point of pleural fields ; antero-lateral corners rounded. Posterior outline short shield-shape. Axis broad, rapidly tapering to a raised blunt extremity situated well forward of posterior margin ; axis high, slightly carinate. 10–12 axial furrows on internal lamina, crowded together at posterior : less than this visible externally. Pleural fields gently arched along mid-line. Anterior border has a low but distinct ridge, parallel with the anterior margin adaxially ; but distally from the point of inflection of the border it diverges and diminishes, thus separating off a narrow triangular area antero-laterally. 3–7 pleural furrows visible, becoming increasingly oblique posteriorly ; do not reach border. 3–4 interpleural furrows faintly visible on internal laminae. Rim furrow a gentle concavity, rising to a wide slightly raised, carinate brim.

REMARKS. *Phillibole polleni* differs from *P. aprathensis* in having a more nearly semicircular headshield ; in having a more smoothly attenuated (i.e. not medianly constricted) glabellar outline ; and in having a shorter pygidial axis. From *Ph. coddonensis* it differs in its larger size, in the shape of the headshield and in the larger relative size of the pygidium.

Phillibole coddonensis (Woodward)

Pl. 3, figs. 1–5.

1895 *Proetus* sp. *a* & *b* Woodward : 648, pl. 28, figs. 7, 8.
1895 *Phillipsia leei* Woodward; Woodward : 646, pl. 28, figs. 1, 1*a*.
1902 *Proetus coddonensis* Woodward : 483, pl. 20, figs. 5, 7–11.

DIAGNOSIS. Small *Phillibole* with broad axis ; some glabellar segmentation ; thorax with eight segments ; very short pygidium.

LECTOTYPE. BMNH. I. 4560 (figured Woodward 1902, pl. 20, fig. 8), here selected as lectotype.

MATERIAL. The specimens upon which this species was founded were collected from North Devon by Hamling & Coomáráswamy, and were subsequently presented to the British Museum (Natural History). Fourteen others from the same collections are to be found in the North Devon Athenaeum, Barnstaple (NDA 812–816). Additional material has been collected from north-east Devon by J. M. Thomas and from north-west Devon by the present author. The total collection examined comprises 3 complete shields, 11 headshields, 11 cranidia, 8 parts of thorax and 15 pygidia.

LOCALITIES AND HORIZON.

1. Coombe (or Combe) Quarry and Wood, Barnstaple. There are a number of old quarries in the neighbourhood of Coombe Wood, which is situated at the eastern end of Codden Hill, 3 miles south-east of Barnstaple, North Devon (Nat. Grid ref. SS 592295). Several of these quarries expose the white chert in which the museum specimens are preserved, but intensive search has failed to yield any more specimens. This group of white cherts occupies a median position in the Chert Formation of the Codden Hill region.
2. Templeton Quarry, Tawstock (Nat. Grid ref. SS 541296). Bed Y, Chert Formation (Prentice 1960).
3. Warrenshill Quarry, Bampton. Bed 16 and 18, Bampton Chert Formation (see p. 238).
4. *Phillibole culmica* regarded as nearly related, was described by R. & E. Richter from the Posidonienschiefer of Aprath, Germany, at an horizon referred to zone IIIβ.

DESCRIPTION. Cephalon. Outline semicircular, length (sag.) being almost exactly twice width (tr.). Glabellar outline sometimes almost parallel-sided, but mostly tapered anteriorly ; base is broad and parallel-sided, attenuation begins abruptly about mid-length of glabella, then becomes parallel sided again anteriorly. Anterior end is bluntly rounded ; anterior portion high, spherical, posterior somewhat lower and flatter. Axial furrow distinct. Occipital furrow nearly straight, or forwardly bowed in centre ; occipital segment narrow (sag.) and strongly inflated. 1p furrow very faint to moderately distinct ; begins well forward and is sharply directed backward : in some specimens joins occipital furrow $\frac{1}{4}$ to $\frac{1}{3}$ along its length : in a very few specimens crosses the occipital furrow and curves outwards across occipital segment to reach axial furrow again near posterior border. 2p furrows sometimes absent, sometimes distinct ; begin at the point of glabella attenuation, and run backwards across glabella more or less parallel to 1p. 3p furrows rarely visible, faint only at sides, directed straight across glabella or slightly forward. Fixed cheek in front of glabella is deeply concave, rising sharply forward to a high enrolled rim ; from this concavity the fixed cheeks rise gently on each side of the glabella, reaching maximum height in the eye region : then fall sharply to occipital furrow. Suture-line begins (α) at point in line with the forward projection of the axial furrows along the sides of the glabella, and swings sharply outwards to β, which lies in the rim furrow in line (exsag.) with or just behind the anterior point of the glabella. Then converges gently with sides of glabella, becoming nearly parallel with these in neighbourhood of 2p furrow. Inflection in eye region very slight. Near to the occipital furrow it swings sharply outwards to cut posterior margin at a point just inside the angle at the base of the spine. Eye small or absent, situated posteriorly of mid-line. Free cheek gently inflated in centre, crossed by strong straight pleuroccipital furrow ; anterior slope of furrow steeper than posterior. Rim furrow broad and deep, rising to flat brim whose edge is sharply enrolled. Doublure broad and flat, carrying 3 or more rows of faint longitudinal striae on underside. Genal spine short, sharply pointed, outer margin deflected slightly outwards.

Thorax. Eight segments only. Axis substantially broader than pleural fields, strongly raised with deep axial furrow. Axial segments W-shaped, especially anteriorly : strongly inflated with a deep transverse furrow at anterior and posterior. Articulating half-ring concealed. Pleural segments broad (exsag.) and short (tr.), sinuous, with rounded truncate extremities. Pleural furrows a deep median excavation, bounded on anterior by strongly diagonal pleural ridge.

Pygidium. Small, narrower than thorax (tr.) at anterior ; short subtriangular in outline. Anterior margin bent forward at axis, but backwards in pleural region. Anterolateral corners rounded. Axis broad anteriorly, broader than pleural region, narrowing rapidly posteriorly to a rounded extremity a short distance anterior of the margin. Faint, low, narrow post-axial ridge rarely developed. Axial rings 5–8, separated by slightly flexuous transverse furrows. First anterior furrow deeper and wider than all others ; posterior furrows diminishing in intensity until posterior extremity is almost smooth. Pleural fields gently raised, indistinct brim furrow and narrow brim with enrolled edge. Pleural furrows 5 to 6, reaching nearly to margin, becoming increasingly oblique and fainter posteriorly. First anterior pleural furrow deeper than others. Interpleural furrows faintly developed laterally only on first 2 to 3 segments. Ventral doublure broad and flat to posterior, narrowing rapidly anteriorly.

Meraspid stage. One specimen and its counterpart (BMNH. In. 22892), collected by Wheelton Hind from Codden Hill, has 5 thoracic segments and clearly represents the meraspid stage. The proportions of the headshield are similar to those of the adult, but the genal spines show a slight outward deflection. There is a slight indication of a pointed anterior margin to the pre-glabellar region. The suture-line has a similar course to the adult, but is proportionately further away from the axial furrow in the median region, and the posterior divergence begins somewhat in front of the occipital furrow. The five thoracic segments are of adult form. The pygidium is small, and shows a posterior bent downwards. Segmentation of the axis is strong ; four axial rings are clearly defined by deep furrows, which gradually decrease in depth towards the rear. Four pleural furrows, and two interpleural, are visible.

REMARKS : The similarity between *P. coddonensis* and *P. culmica* was acknowledged by R. & E. Richter (1939 : 110), but they maintained the identity of the latter on the grounds that *P. coddonensis* has a less-diminishing glabella, and a tail with a well developed brim. The former feature is somewhat variable in *P. coddonensis*, but in the material examined there are many specimens which can be matched in this feature with Richter's illustrations of *P. culmica*. Photographs of the holotype of *P. culmica* (kindly supplied by Dr. G. Hahn) show however that these specimens have a longer and more elliptical headshield, a more strongly attenuated glabella, and a narrower (tr.) posterior section of the fixed cheek than *P. coddonensis*. The appearance of a brim to the tail in Woodward's illustrations is seemingly due to the preservation as a mould, which leave a space between the inner and outer moulds of the edge of the doublure. In reality *P. coddonensis* has no more brim than *P. culmica*.

Osmólska (1962 : 75) has referred *P. culmica* to the subgenus *Macrobole*. The present species resembles *M. drewerensis* (the type species) in the lobation of the glabella, but the strong segmentation of the pygidium in *Macrobole* is a major point of distinction. The pygidium of *P. coddonensis*, while unlike that of almost any other contemporary trilobite in form, does have the accentuated anterior furrow and the rather indistinct pleural furrows of *Phillibole*. The outline of the glabella and the course of the suture line are similar to those of *Phillibole aprathensis* (the type species), but *coddonensis* is distinguished by the presence of glabellar segmentation. It should be borne in mind, however, that in some species of *Phillibole* (e.g. *P. polleni* see p. 221) the glabella is smooth on the outer, and segmented on the inner lamina. Since the type material of *P. aprathensis* is preserved in shale, the holotype presumably preserves the outer lamina, while all the material of *P. coddonensis* consists of moulds of the inner. The presence of only eight thoracic segments, the breadth of the axis and the very small pygidium distinguish this species from all other species of *Phillibole*.

DIMENSIONS (in mm.)

Cephalon :

	L. (sag.)	W. (tr.)	Lg. (sag.)	Wg. (tr.)	L. (genal spine)
BMNH.					
I. 4560	3·8	5·8	3·0	2·0	1·0
I. 4561	4·9	8·1	4·2	3·5	0·9
I. 4564	4·2	11·5	2·8	—	—
I. 4565	4·0	9·0	3·5	3·1	—
I. 4571	4·0	5·8	—	2·0	1·0
KCL.					
t. 170	3·6	5·0	—	—	0·9
t. 191	4·8	—	3·4	2·2	0·9

Thorax :

	L. (sag.)	W. (tr.)	W. ax. (tr.)
BMNH. I. 4560	3·0	4·8	2·1 ant. 1·6 post.

Pygidium :

	L. (sag.)	W. (tr.)	L. ax. (sag.)	W. ax. (tr. ant.)
BMNH.				
I. 4560	1·8	3·8	1·6	1·2
I. 4564	2·3	6·1	1·8	2·7
In. 18409	2·1	5·0	1·5	2·0
KCL.				
t. 188	3·3	6·1	—	—
t. 208	3·6	4·4	—	—

Genus ***LIOBOLE*** R. & E. Richter 1949

The genus *Liobole* was proposed as a subgenus of *Phillibole* by R. & E. Richter (1949 : 71) with *Phillipsia glabra* Holzapfel 1889 as type species. The name was later raised to generic rank by R. & E. Richter (e.g. 1951 : 231), Struve (*in* Moore 1959) and Osmólska (1962). The *Liobole* group seems more closely linked with the genus *Liobolina* (see Osmólska 1962 : 76, 92) than with *Phillibole* s.s., so that its generic rank seems to be substantiated.

Liobole glabra (Holzapfel)

Pl. 3, figs. 1–5.

1889 *Phillipsia glabra* Holzapfel : 73, pl. 8, fig. 23.
1895 *Griffithides acanthiceps* Woodward : 674, pl. 28, figs. 5, 5*a*.
1902 *Phillipsia* sp. Woodward : 482.
1902 *Proetus* sp. Woodward : 484, pl. 20, fig. 1.
1949 *Phillibole* (*Liobole*) *glabra glabra* (Holzapfel) ; R. & E. Richter : 72, pl. 1, figs. 1–3.
1949 *Phillibole* (*Liobole*) *glabra hiemalis* R. & E. Richter : 74, pl. 1, figs. 4–11, (subsp. n.).
1960 *Phillibole* (*Liobole*) *glabra glabra* (Holzapfel) ; Prentice : 271, pl. 12, fig. 1.

DIAGNOSIS. As for R. & E. Richter 1949 : 72.

MATERIAL. Three cranidia (BMNH. It. 381, It. 1436, It. 1437*a*, *b*, KCL t175–6) one with thoracic segments and a fragment of free cheek attached, both somewhat crushed. One specimen (NDA 822 and counterpart BMNH. In. 33775) with thoracic segments and slightly displaced pygidium : three separate pygidia (BMNH. I. 1438, I. 4562, In. 18411). Two separate free cheeks and counterparts (BMNH. I. 3020, I. 3216).

LOCALITIES AND HORIZON.

1. Park Gate Quarry, Tawstock. Nat. Grid ref. SS 555297. Probably from Bed X, correlated (Prentice 1960 : 273) with zone II/IIIα, at a low horizon within the Codden Hill facies of the Chert Formation.

2. Codden Hill ; Hannaford Quarry ; Templeton Quarry, Tawstock. All these localities lie within the Codden Hill Cherts, but the last-named locality is doubtful, as all other fossils collected from this quarry belong to a higher horizon.

3. Warrenshill Quarry, east of Bampton, North Devon (Nat. Grid ref. SS 978222), Bed 15, Bampton Chert beds (see p. 238), J. M. Thomas collection.

Description of North Devon material.

Cephalon. Outline probably semicircular, shorter (sag.) than wide (tr.) Glabellar outline broad, attenuated forward, anterior end almost semicircular in plan. Posterior margin of glabella convex forward, so that occipital segment is very narrow (sag.) in centre ; this margin has a sharp raised rim. Occipital glabellar furrow distinct and deep in central third, branches laterally ; posterior branch fades away rapidly, anterior branch (1p) runs forward and nearly reaches axial furrow. These two branches enclose a lobe which is pear-shaped in outline, moderately raised laterally. At the posterior margin of the occipital segment is a deep furrow bounded posteriorly by a very narrow posterior rim ; this furrow meets the axial furrow and the posterior fixigenal furrow at a deep triangular apodemal pit. Second glabellar furrow (2p) starts at or near the axial furrow, runs gently backwards and deepens, then swings sharply backwards to join 1p and occipital furrows at their point of divergence, becoming fainter as it does so. Third furrow (3p) faint, nearly parallel with 2p but confined to sides of glabella and shows no backward swing. Axial furrow clear but not deep. Preglabellar field narrow, concave, rising steeply to a sharply enrolled rim higher than the glabella. Anterior doublure broad, carries four parallel longitudinal striae on inner side. Anterior of fixed cheek faintly concave in continuity with concavity of preglabellar field, then rises until nearly flat along sides of glabella : rises again slightly just in front of pleuroccipital furrow. Pleuroccipital furrow broad and deep, widens laterally ; anterior slope steeper than posterior ; course straight. Occipital segment of fixed cheek very narrow, inflated, bounded posteriorly by very deep furrow. Facial suture begins (α) close to mid line, cuts very obliquely across border in an almost straight line to β, which lies only just behind the line of the anterior of the glabella. From β, which is gently rounded, suture curves inwards to within a short distance of the axial furrow. There is a shallow palpebral lobe ($\gamma - \epsilon$) situated well forward ; from ϵ suture diverges in a gentle outwardly concave curve to cross occipital furrow and reach ω wide of the axial region. Posterior part of the fixed cheek is thus broadly triangular in shape.

Free cheek gently, flatly inflated. Margin broad, gently raised, with a very indistinct border furrow ; genal angle rounded, produced into short, spatulate extension. Pleuroccipital furrow sharp near axis, dies out abruptly at border furrow. Eye visible on inner test lamina only, no corresponding impression on inside of outer laminae, nor presumably on dorsal exterior. Eye platform very slightly raised, situated well forward near the border furrow. Inner side of eye practically straight, outer side strongly convex, so that eye is nearly semi-circular ; surface finely reticulate, composed of two series of intersecting concentric ridges, centred at points $\frac{1}{4}$ and $\frac{3}{4}$ along inner border of eye ; each interspace so formed bears a central circular depression. Doublure of the free cheeks broad, strongly enrolled, diminishing in width posteriorly. Inside of doublure carries fine sub-parallel striations, which are not present on the underside of the dorsal margin.

Thorax. Axis broad, equal in width or somewhat wider than the pleural regions ; somewhat more raised than pleurae. Axial ring shows a strong transverse concavity ; anterior is a low ridge higher along median line than laterally, where it is largely covered by the posterior of the preceding ring. The concavity is steeper on its anterior side ; behind, it rises gently to a high transverse ridge, which terminates at each end in a boss at the axial furrow. Beneath this posterior ridge in the median line the carapace is deeply infolded ; laterally this fold opens out so that the ring shows a posterior sulcus bounded behind by a low triangular flange. The posterior margin of this flange is continuous with the posterior margin of the pleural segments. Pleural segments are flatly arched, nearly straight with blunt rounded extremities ; each has a transverse concavity bounded by a high posterior ridge ; the concavity shallows laterally and is crossed by an oblique ridge which commences anteriorly near the axial furrow and terminates near the posterior side at the pleural extremities. This ridge is steeper on its posterior side, and slightly lower laterally than near the axis.

The maximum number of segments found articulated is eight.

Pygidium. Shield-shaped in outline, somewhat wider than long. Anterior margin bowed forward in axial region, gently bowed backwards in pleural ; antero-lateral angles rounded. Axis moderately broad, slightly wider than pleural region at pygidial anterior ; axial furrows straight, so that axis is regularly tapering ; axial furrows and identity of axis become less pronounced posteriorly. Axis terminates abruptly at a rounded extremity before reaching posterior margin, continues as a very low postaxial ridge. Anterior of axis bears a deep, forwardly convex, transverse furrow, which separates off a high, narrow, anterior axial ring. Axial rings faint, up to 12 sometimes faintly visible. Paired pygidial muscle apodemes visible on internal mould at ends on first 6 transverse furrows. Pleural regions gently inflated, nearly smooth. Anterior has a deep transverse furrow, bounded by a high, narrow, anterior ridge ; this furrow lies parallel with the anterior border from axis to midpleural (tr.) region, then swings sharply backwards, so that antero-lateral corner is a narrow triangular flange. Posterior pleural furrows very faint (9+), separated by equally faint interpleural furrows ; both sets are just visible laterally as far as the border furrow. Border furrow faint, accentuated by crushing, separating a moderately broad flat brim. Ventral doublure broad, strongly enrolled, slightly wider at posterior extremity ; bears faint traces of internal longitudinal striation.

REMARKS. The features which distinguish the subspecies *L. glabra glabra* and *L. glabra hiemalis* (R. & E. Richter 1949) are unfortunately most susceptible to modification by crushing and distortion. It has been thought advisable therefore to refer the North Devon specimens only to the species without attempting further subdivision. They are distinguished (*a*) from *L. coalescens* R. & E. Richter by the much clearer development of " occipital-solution " and the more clearly defined axial region, (*b*) from *L. glabroides* R. & E. Richter by the broader and less attenuating glabella, and by the broadly triangulate free cheeks, (*c*) from *L. subaequalis* (Holzapfel) by the furrowed glabella and (*d*) from *L. zarembiensis* Osmólska by the narrower free cheeks.

Thoracic segments have rarely been described in the Cyrtosymbolids, and never previously for a species of *Liobole*. There is a tendency for the ventral anterior doublure to adhere to the free cheek when this is separated from the cranidium ; this gives the appearance of a short spatulate " genal spine ", and resulted in Woodward (1895, text-fig. 5) illustrating a specimen in an inverted position. The present account shows that *L. glabra* has a rounded, slightly extended genal angle similar to other members of the genus (e.g. *L. subaequalis* Holzapfel).

Genus ***SPATULINA*** Osmólska 1962

Type species. *Phillipsia spatulata* Woodward 1902.

The genus *Spatulina* with *S. spatulata* as type species, includes also *Phillibole*? (*Cystispina*) *nasifrons* R. & E. Richter 1949 and *Phillibole* (? *Cystispina*) sp. nov. Prentice 1960 (Osmólska 1962 : 74, 90, 180–181).

Emended diagnosis. Cyrtosymbolids with stout, hollow, genal spines. Cylindrical glabella with moderately distinct or faint dorsal furrows. Occipital glabellar segment of equal length sagitally and exsagitally, occipital furrow complete and unbranched. Fixigenae very narrow, with an abrupt forward slope anteriorly (based on diagnosis by Osmólska 1962 : 180).

Osmólska suggests that the resemblances of this group of *Cystispina*, in which *S. spatulata* was formerly placed by R. & E. Richter, are merely superficial, and that the cranidial structure marks them out distinctively from that genus. Certainly the three known species of *Spatulina* have very similar cephala, the only points of distinction being the shape of the librigenal spines, and slight differences in the shape of the glabella. The thorax is known only in *S. longispina* sp. nov., in which it consists of 9 segments. The pygidium is known from all three species, and is, characteristically, nearly smooth, with a high tapering axis terminating some distance in front of the posterior extremity, which falls away rapidly from the tip of the axis. The pleural fields have only a very narrow indistinct rim.

This small, closely knit group, has a very restricted range geographically and stratigraphically. It is known only from the Chert Formation of North Devon, and from the Erdbach & Belecke limestones in the Rhineland ; *Pericyclus* Zone (II).

Spatulina spatulata (Woodward)

Pl. 6, figs. 5, 6, Text-fig. 2.

1902 *Phillipsia spatulata* Woodward : 482, pl. 20, figs. 3, 4.
1939 *Phillibole* ? (*Cystispina*) *spatulata* (Woodward) R. & E. Richter : 107, text-figs. 17, 18.
1960 *Phillibole* ? (*Cystispina*) *spatulata* (Woodward) ; Prentice : 271, pl. 12, fig. 9.
1962 *Cystispina spatulata* (Woodward) ; Osmólska : 180.

Diagnosis. *Spatulina* with short, bluntly rounded, hollow spines. Glabella parallel-sided.

LECTOTYPE. BMNH. I. 3215 selected by R. & E. Richter (1939) from among the syntype material cited but not figured by Woodward (1902).

MATERIAL. In addition to the lectotype three specimens described by Woodward are preserved in the British Museum (Natural History): I. 4572 (Woodward 1902, pl. 20, fig. 4), I. 3219 and I. 3223. Other specimens from the Woodward collection are in the North Devon Athenaeum : NDA 802, the original of pl. 20, fig. 3 and its counterpart NDA 803, NDA 804–805. Additional material collected by the writer is now in the British Museum (Natural History) nos. BNMH. It. 1439*a*, *b*.

LOCALITY AND HORIZON. The species is only known from the Chert Formation of Codden Hill, Combe Wood and Tawstock, Barnstaple, North Devon. Specimens BMNH. It. 1439*a*, *b* and I. 3223 came from Park Gate Quarry, Tawstock, where Bed X, of Zone II/IIIα age is exposed (see p. 238) ; on the latter specimen also occurs *Macrobole* cf. *brevispina* (see p. 238) indicating a Zone II horizon.

DESCRIPTION. A full description was given by R. & E. Richter (1939 : 108) ; the following are additional features seen on the new material:

Occipital segment, which is nearly parallel sided transversely, sometimes carries a small median tubercle ; occipital furrow a little fainter medianly than at sides. Lateral glabella furrows distinct on internal mould ; pre-occipital lobe long (exs.), triangular. Preoccipital (1p) furrow begins at axial furrow, curves gently back, then more sharply to terminate abruptly close in front of occipital furrow. 2p lobe narrower than 1p, 2p furrow parallel to 1p ; 3p furrow faint, parallel to 2p but shorter. 2p furrow begins at axial furrow at point almost halfway along (exs.) the glabella length.

Pregabellar border has 2 or more fine longitudinal striae on inner side. Fixed cheeks have a gentle anterior concavity, rising along the sides of the glabella to the highest point near the 2p furrow ; posterior falls again to pleuroccipital furrow.

Free cheek gently inflated in centre ; an obscure concavity in front deepens to become a moderately deep rim furrow posteriorly. Pleuroccipital furrow distinct, meets rim-furrow at 90°, and the two are produced for a short distance along the dorsal face of the genal spine. Rim of free cheek slightly raised, margin sharply geniculate, so that exterior of free cheek is flattened flange, which continues on to outside of genal spine. Doublure broad, strongly enrolled, with 7–8 subparallel longitudinal striations on the inside of the lower fold.

Genal spine short, approximately half length of cephalon (sag.) ; outer lateral side of spine flattened, in continuity with flattening of the side of the cephalon. Spine at genal angle nearly circular in cross-section ; medianly is slightly inflated and terminates sharply in a slightly mucronate chisel-shaped end, whose edge lies nearly vertically to the plane of the dorsal shield. Dorsal surface of spine gently rounded, impressed for a short distance by the continuation of the coalesced marginal and pleuroccipital furrow ; falls slightly at point. Interior of spine bears fine longitudinal striae in continuity with those of the interior of the doublure.

Thoracic segments unknown.

Pygidium shorter than wide, shield-shaped. Anterior margin has a narrow raised rim ; antero-lateral angles rounded. Axis strongly raised, rapidly tapering,

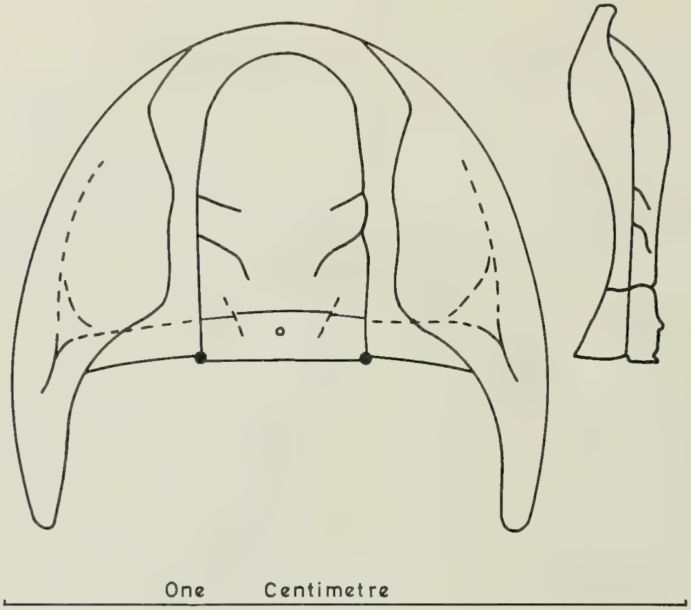


FIG. 2. *Spatulina spatulata* (Woodward). Reconstruction.

terminating in a high, blunt, rounded end. Axial furrow distinct. 8 or more faintly defined axial rings, bearing faint traces of interior of paired pygidial muscle impressions. Pleural regions gently inflated, fall away rapidly behind ; narrow, gently raised rim with an indistinct border furrow. Pleural furrows very faint.

REMARKS. As indicated by Osmólska (1962 : 180) the differences between *S. spatulata* and *Cystispina cystispina* are sufficient to warrant their generic separation. These differences are in the shortness of the preglabellar field, the non-tapering glabella, and the narrow fixigenae in *S. spatulata*. On the other hand, the distinctness of the glabellar furrows is not a point of difference, as in both genera these are clear on the internal mould and indistinct on the interior (and presumably on the dorsal exterior) of the carapace. The pygidia of the two genera are also very similar. From *S. longispina* sp. nov. (see below) *S. spatulata* differs in the shape of its spines and its parallel-sided glabella ; from *S. nasifrons* (R. & E. Richter 1949) it differs in that the latter species has a more prominent, slightly constricted glabella and (*fide* Osmólska 1962 : 180, text-fig. 5*f*) a very broad spine.

Spatulina longispina sp. nov.

Pl. 6, figs. 1–4 ; Text-fig. 3.

1895 *Griffithides longispinus* Portlock ; Woodward : 647, pl. 28, fig. 6.
1960 *Phillibole* (? *Cystispina*) sp. nov. Prentice : 271, pl. 12, fig. 2.

DIAGNOSIS. Moderately large *Spatulina* with long, hollow, pointed librigenal spines. Glabella slightly tapering.

HOLOTYPE. One nearly complete specimen, a somewhat crushed internal mould (BMNH. It. 1440*a*) from Park Gate Quarry, Tawstock, North Devon.

MATERIAL. Holotype and counterpart (BMNH. It. 1440*b*) : two separated free cheeks, one pygidium and other fragments on a single slab (BMNH. It. 1441): a nearly complete specimen with crushed cranidium and displaced free cheeks (BMNH. I. 4573*a*) and partial counterpart (BMNH. I. 4573*b*) : parts of cephala (NDA. 809, NDA. 825).

LOCALITY AND HORIZON. The specimens (KCL 170–178, BMNH. It. 1440–41) collected by the author are from Bed X in Park Gate Quarry, Tawstock (see p. 238), of II–IIIα zone age. Specimen BMNH. I. 4573 came from the Chert Formation, Coddon Hill, and those in the North Devon Athenaeum are from Combe Wood and Hannaford from similar horizons.

DESCRIPTION. Cephalon. Outline, when restored, nearly semicircular ; length (sag.) of holotype 11·1 cms., width at occipital region 15·2 cms. Glabella tapers slightly forward, slightly constricted medianly, with oval rounded anterior, moderately high. Occipital furrow clear and nearly straight, continuous across cephalon, tripartite, occipital segment same width (sag.) throughout. No median occipital spine. Axial furrow distinct, glabella raised above fixed cheeks. Preoccipital lobe only slightly longer than occipital segment. 1p glabellar furrows very vague, directed backwards to the mid-point of the occipital furrow. Pre-glabellar field very narrow, upwardly inclined then bent over to form a very narrow brim. This brim continues along the anterior margin of the fixed cheeks, where a deep concavity is continuous with the concavity of the preglabellar field. Facial sutures begin (α) at a point within the projection of the axial furrow at the glabellar sides then swing outwards very obliquely across the brim to β, thence curve inwards to γ which lies close to the axial furrow about half way along (exsag.) the glabella. Palpebral lobes not evident ; suture line follows axial furrow for short distance, then swings outwards gently to ω, which lies near to the internal angle of the genal spine.

Free cheeks nearly flat except for narrow brim ; occipital furrow clear becoming fainter laterally. Genal angle with long spine (7·5 mm. in holotype) circular in cross section for most of its length, then narrowing rapidly to a slightly mucronate point. Anteriorly the dorsal face of the spine bears a deep triangulate concavity, the continuation of the occipital furrow. The spine is hollow with faint internal longitudinal striations. Doublure broad, hollow, in continuity with genal spine ; carries 4 to 5 longitudinal striations on its underside.

Thorax. The remains of only 4 segments are preserved in the holotype, but the specimen figured by Woodward (BMNH. I. 4573*a*) is complete and shows 9 segments. The axis is wide (4·5 mm. in holotype) slightly wider than original to width of the pleurae, moderately raised. Axial ring has deep transverse furrow slightly anterior of the median (sag.) line ; anteriorly a narrow, posteriorly a broad, raised rim. Pleural regions less raised than axis, with broad shallow pleural furrow, and bluntly rounded pleural extremities.

Pygidium. Elongate, hemi-elliptical in outline, with strongly raised, tapering, axis separated from somewhat flatter pleural fields by a sharp axial furrow. Length

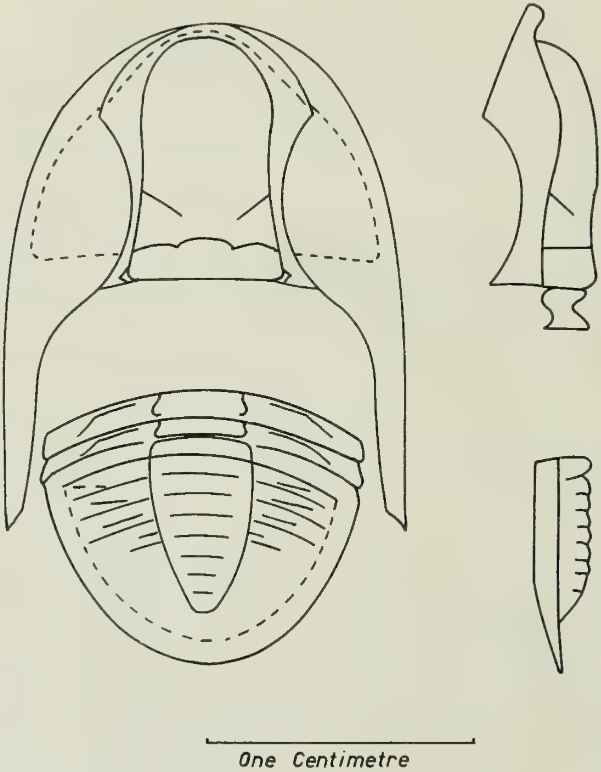


Fig. 3. *Spatulina longispina* sp.n. Reconstruction.

(holotype) 9·9 mm. (sag.), width at anterior border 11·9 mm. (tr.), width of axis 4·5 mm. Axis rapidly tapers to a sharply rounded, strongly elevated point, which lies a short distance (2 mm. in holotype) in front of the posterior of the pygidium. Axial rings 9–11, clearly defined at anterior becoming effaced behind. Pleural fields nearly flat, with traces of four oblique pleural furrows and three interpleural furrows anteriorly. Margin gently raised, no border furrow. Doublure sharply infolded, 1 mm. wide, with faint longitudinal striae internally.

Remarks: The species may be distinguished from *S. spatulina* by its long, cylindrical, pointed spines, by its slightly tapering glabella with very faint lateral furrows, and by the more distinct segmentation of the pygidium. These same characters distinguish it from *S. nasifrons* (R. & E. Richter).

Specimen BMNH. I. 4573 was assigned by Woodward to *Griffithides longispinus* Portlock. However, the large eyes and the absence of a pre-glabellar field in Portlock's species preclude the inclusion of the present specimens. The trivial name *longispinus* is, nevertheless, apt, and is employed here.

Genus *TYPHLOPROETUS* R. Richter 1913

Type species. *Typhloproetus microdiscus* R. Richter, 1931.

This genus includes 14 species ranging in age from the Middle Famennian to the Lower Visean. They have in common a tapering glabella, anteriorly divergent often ankylosed sutures, vestigial eyes and a characteristically laterally narrowed occipital glabellar segment.

Typhloproetus cephalispina sp. nov.

Pl. 2, figs. 4, 6.

Diagnosis. Typhloproetids with nearly semicircular cephalon, bearing a short spine at anterior extremity. Glabella with one pair of lateral furrows; eyes vestigial. Suture line cuts anterior border near midline, anterior part widely divergent.

Holotype. Cephalon, BMNH. It. 1442 (J. M. Thomas coll.), Bed 18, Chert Formation, Warrenshill Quarry, Bampton, North Devon (see p. 238).

Material. In addition to the holotype, one other cephalon with counterpart showing three thoracic segments attached (BMNH. It. 1443*a*, *b*) from same horizon and locality.

Horizon. Upper Visean, Zone IIIβ.

Description. Cephalon semicircular in outline; holotype length (sag.) 2·0 mm., width 4·0 mm. Glabella broad and flat posteriorly, moderately high and rounded anteriorly; width (holotype) at occipital segment 1·6 mm.; length (sag.) 1·9 mm. Axial furrow clear anteriorly, faint posteriorly. Glabellar outline gently tapering, with strongly rounded anterior; constricted medianly. Occipital furrow deep, the anterior slope being especially steep, curved forward in centre. Occipital segment narrows laterally; strongly inflated with a steep posterior rim. 1p lateral furrows distinct, begin at axial furrow far forward, and are strongly inclined backwards towards, though not reaching, the mid-point of the occipital furrow. Preoccipital lobes are thus long and triangular. In front of 1p furrows glabella is strongly inflated, pyriform. Narrow preglabellar field, strongly concave, rising to a high anterior rim, in centre of which is a short, bluntly rounded cephalic spine, directed upwards and forwards. Fixed cheeks rise from their anterior concavity to faint palpebral lobes situated parallel with mid-line (sag.) of glabella. Posterior of fixed cheek deeply incised by occipital furrow.

Suture line ill-defined, probably ankylosed. Cuts anterior margin (α) very near to centre of cephalic anterior, swings outwards very obliquely to β which lies in the border furrow; then curves in broad curve to near axial furrow near 1p lateral furrow; subparallel to axial furrow for a short distance posteriorly, then diverges in pleuroccipital region to cut posterior margin of headshield at a point (ω) midway between axial furrow and lateral margin of headshield.

Free cheek gently inflated centrally, falling to a broad marginal concavity anteriorly and laterally and steeply to a straight pleuroccipital furrow behind. Eye platform, small, raised, elongate, situated a little in front of the mid-line (sag.). Rim of cephalon sharply upturned, folded over to a wide doublure which carries 3 subparallel longitudinal striations on the underside. Small pointed genal spine.

Thorax with broad axis, more than a third of the width (tr.) of the carapace. Axial ring high, strongly curved sagitally with a deep anterior transverse furrow separating the articulating half-ring. Pleural regions gently inflated, with their lateral extremities bent sharply ventrally. Pleural furrows deep and wide, extending subcentrally the whole length of the pleurae.

Pygidium unknown.

REMARKS. The species is included in *Typhloproetus* on the basis of the form and nature of the facial sutures, the vestigial eyes, and the shape of the occipital glabella segment. It differs from the genotype, *T. microdiscus* in its more prominent glabella, its more widely divergent facial sutures, and the shorter cephalic outline. From *T. dietzi* R. & E. Richter it differs in having a less tapering glabella, and a narrower anterior rim. Neither of these species has a procranidial spine. *T. koslowskii* Osmólska, and ? *T. angustigenalis* Osmólska (which shows some indication of an anterior point) have more elongate glabellae than the present species.

Genus ***DIACORYPHE*** R. & E. Richter 1951

The genus *Diacoryphe* with type-species *D. pfeifferi* includes also *D. gloriola* Richter : both are from the Zone I horizon of Germany (R. & E. Richter 1951 : 252). Osmólska (1962 : 177) included a new species *strenuispina* in this genus on the basis of cranidial similarities, although the thick librigenal spine and strong anterior border would exlude it from the generic diagnosis of R. & E. Richter. The British species *vandergrachtii* has many similarities to *strenuispina*, but differs even more from the type species of *Diacoryphe*. It is therefore, only doubtfully assigned to this genus.

Diacoryphe? vandergrachtii (Woodward)

Pl. 7, figs. 1–5 ; Text-fig. 4.

1894 *Phillipsia van-der-Grachtii* Woodward : 485, pl. 14, figs. 1–6.

DIAGNOSIS. Small trilobites possessing a pyriform glabella with effaced axial furrow at posterior ; strong anterior border-ridge ; long inflated genal spines ; thorax with 8 segments ; and strongly segmented pygidium.

MATERIAL. The six specimens described and figured by Woodward (1894) are preserved in the British Museum (Natural History). The specimen figured by Woodward (1894, pl. 14, fig. 3) is here selected as lectotype. The specimens are preserved in shale, either as crushed carapaces showing the external view of the dorsal side, or as external moulds of the same. The specimens were collected from the same locality as those of *Phillibole polleni*, whose stratigraphical horizon (see p. 238) is at or just below the B_1—B_2 zonal boundary.

Description. Outline of carapace elliptical, nearly twice as long as wide. Cephalic outline parabolic, widest at posterior margin, wider than long. Glabella sharply demarcated from fixed cheek anteriorly, but posteriorly the axial furrow is poorly defined. Anterior of glabella rounded, widest (tr.) part $\frac{1}{3}$ of length (sag.) from anterior ; behind this gently narrowing to a minimum width (tr.) at the occipital furrow. Occipital lobe of glabella widens again to attain width of the anterior. Occipital furrow faint but continuous across glabella, bent forward in centre ; no trace of other furrows. Preglabellar field narrow, rising rapidly to a broad enrolled rim, which carries three longitudinal subparallel ridges. Facial suture cuts anterior margin at a point (α) just inside the forward projection of the widest part of the glabella ; from thence it swings sharply outwards to β which lies almost within the marginal furrow. Swings inwards more sharply to γ, which is broadly rounded and lies very close to the axial furrow at the point of maximum glabellar width. From γ the suture is gently convex outwards swinging inward and near to the axial furrow at ϵ, which lies just in front of the occipital furrow. On crossing the occipital furrow the suture line runs sharply outwards in a straight line, to cut the posterior margin of the headshield (ω) just inside the genal spine. Fixed cheek is thus very wide in front and very narrow behind ; in profile almost flat except for the raised rim. Free cheeks smooth, gently raised in centre, falling to a broad deep furrow inside a raised rim. This rim is broader anteriorly, where it is continuous with the rim of the fixed cheek, becomes sharper and narrower posteriorly, and at genal angle passes into the librigenal spine. This spine is as long as the headshield, reaching to the posterior thoracic segment ; broad and inflated, terminating in a blunt rounded extremity. The interior angle with the posterior margin of the headshield is rounded. Pleuroccipital furrow of free cheek faint and broad.

Thorax of eight segments ; axial region strongly raised, separated from pleural regions by a sharp axial furrow. Axis one third width (tr.) of carapace at anterior, narrowing slightly posteriorly. Axial rings nearly parallel-sided (tr.) slightly embayed, posteriorly and bent forward anteriorly ; articulating half-ring not visible. Pleural segments parallel-sided, slightly flexed backwards from a point close to axial furrow ; extremities bluntly rounded. Pleural furrows faint ; in median (ensag.) position near axial furrow, then directed obliquely backwards across segment, becoming effaced halfway along (tr.).

Pygidium sub-triangular, $1\frac{1}{2}$ times broader (tr.) than long (sag.) : anterior margin strongly and evenly curved forward. Axis sharply raised, separated by a sharp axial furrow from the more moderately upcurved pleural regions. Axis tapers rapidly, terminating in a triangular point a short distance in front of the posterior of the pygidium. 8 or more axial rings, separated by strong, straight furrows. Pleural fields crossed by 6 furrows, becoming progressively weaker and more oblique towards the posterior. All pleural furrows die out at rim, which is moderately broad and slightly flattened. Postaxial region bent ventrally, no postaxial ridge.

Remarks. The genus *Diacoryphe* is almost unique among Carboniferous trilobites in showing posterior effacement of the glabella, and it is for this reason that the species *vandergrachtii* is consigned to this genus. It differs from the type species, *D. pfeifferi*, in the less widely expanded anterior part of the fixed cheek, on the long palpebral lobes, and in the strong anterior border. It resembles *D. strenuispina* Osmólska in having a strong, inflated genal spine. The pygidium, with its strong segmentation, is more like that of a Phillipsiid, than that of *D. pfeifferi*. It seems likely that a new genus is needed for the reception of the British species.

III STRATIGRAPHICAL CONCLUSIONS

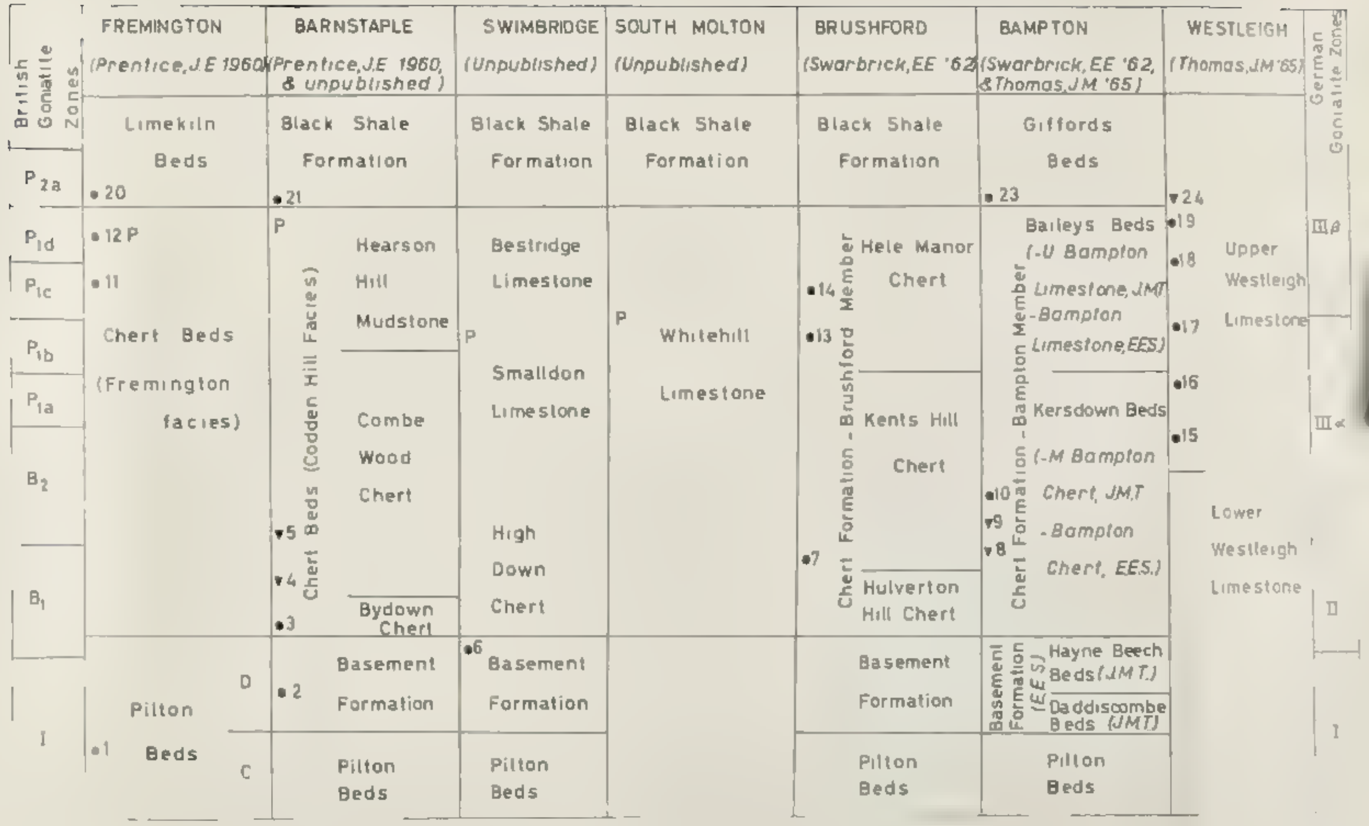
The trilobites described here occur mostly in a region of great structural and stratigraphical complexity, which has as yet been very incompletely unravelled. The diagram (Table 1) attempts to record the succession in various areas of North Devon, in so far as it has been resolved. With few exceptions the trilobites occur in a group of beds of distinctive pale grey or white colour, which occupies a median position in the Chert Formation. The Chert Formation is underlain by the Basement Beds, and these by the Pilton Beds. Goldring (1955), on goniatite and trilobite evidence has classified the top of the Pilton Beds with the *Protocanites* Zone (I) The occurrence of *Protocanites* cf. *lyoni*, probably in the Basement Formation (Prentice & Thomas 1965) indicates that the *Protocanites* Zone extends above the Pilton Beds. The occurrence of *Pericyclus* aff. *homoceratoides* at Swimbridge, also in beds which are probably Basement Formation, indicates that this formation also includes the base of zone II (Butcher & Hodson 1960). The top of the Chert Formation is in many places defined by the " *G. spiralis* " band, of P_1—P_2 age (Prentice 1960), indicating that this Formation extends throughout most of zones II and III of the German sequence.

Within this succession it seems possible to recognize five successive trilobite faunas. The lowest occurs near the base of the pale chert group, probably close above the Basement Formation, and, so far, has been found in only one place. It yields *Macrobole* aff. *laticampa*, which occurs in Zone I in Poland. The second is more widespread : it is the fauna described by the author (Prentice 1960) from Bed X in Park Gate Quarry, Tawstock. This bed is characterized by the occurrence of the genus *Spatulina*, whose only representative outside Devon occurs in Zone II of Germany (Richter, R. & E. 1949). Associated with this is *Liobole glabra* and *Macrobole* cf. *brevispina*. *Liobole glabra* also occurs at Warrenshill Quarry, Bampton, in white cherts referred by Thomas to the Kersdown Beds (Webby & Thomas 1965). These cherts lie immediately below similar beds with *Phillibole coddonensis*, which forms the chief element of the third trilobite fauna. This has been found in place also in Templeton Quarry, Tawstock (Bed Y, Prentice 1960). The occurrence of both the *Spatulina* fauna and the *P. coddonensis* fauna at various localities (Coombe Wood, Hannaford, Codden Hill) indicated by museum specimens, suggests that these two faunas are widespread and stratigraphically are closely superposed. *Phillibole aprathensis* is also recorded from these localities, but there is some evidence to suggest that it may occur in and characterise a higher horizon. For example, it occurs in a loose block above the beds exposed at Warrenshill Quarry, Bampton ; and at a high horizon in cherts in the Chudleigh region. The highest fauna is that represented by *Phillipsia leei*, a species constantly found in the " *spirale* band " which marks a very widespread depositional change in south-west England.

Explanation of Table 1

Numbers in circles represent goniatite faunas, those in squares contain trilobites. The following list indicates only the latest reference to the fossils.

[illegible] Appendix : 48).	Pilton Beds.
[illegible] Schmidt.	Tutshill farmyard.
[illegible]	
[illegible] mas, J. M. (1965 : 34).	
[illegible] Meek & Worthen.	Well near Mt. Sandford, Barnstaple.
[illegible]	Bydown Quarry, Swimbridge.
[illegible]	Park Gate Quarry, Tawstock.
[illegible] H. Schmidt	
[illegible] H. [illegible]	
[illegible] E. Richter	
[illegible] *ata* Woodward (as *Ph.* ? (*Cy.*) *spatulata*).	
[illegible] as *Ph.* ? (*Cy.*) sp. nov.)	
[illegible] *bole*) cf. *brevispina* Osmólska (as *Waribole*) cf. *aequalis*).	
[illegible]	Templeton Quarry, Tawstock.
[illegible] Woodward	
[illegible]	Railway Cutting, Swimbridge
[illegible]	
[illegible]	Kents Hill Quarry, Dulverton.
[illegible] *ssimus* (de Koninck).	
[illegible] Thomas, J. M. (1965) and the	
[illegible] E. Richter	Bed 15, Warrenshill Quarry, Bampton.
[illegible] *onensis* Woodward	Beds 16 & 18, Warrenshill Quarry, Bampton.
[illegible] *tus cephalispina* sp. nov.	Bed 18, Warrenshill Quarry, Bampton.
10. Webby, B. & Thomas, J. M. 1965.	
Bollandites sp.	Kersdown Quarry, Bampton.
11–14. Butcher, N. E. & Hodson, F. (1960 : 77).	
11. *Goniatites sphaericostriatus* Bisat	Fremington.
12. *Girtyoceras burhennei* (Schmidt)	Fremington.
13. *Goniatites falcatus* Roemer	Hele Quarries, Dulverton.
14. *Goniatites* of the *concentricus/striatus* group	Hele Quarries, Dulverton
15–19. Prentice, J. E. & Thomas, J. M. (1960 : 6, 7).	
15. *Goniatites hudsoni—antiquatus* group	Westleigh Quarries.
16. *Goniatites crenistria* Phillips	Westleigh Quarries.
17. *Goniatites falcatus* Roemer	Westleigh Quarries.
18. *Hibernicoceras carraunense* Moore & Hodson *Sudeticeras crenistriatus* Bisat	Westleigh Quarries.
19. *Neoglyphioceras spirale* (Phillips) *Sudeticeras splendens* (Bisat)	Westleigh Quarries.
20 & 21 Prentice, J. E. (1960 : 275).	
Neoglyphioceras spirale (Phillips)	Fremington Pill, and Tawstock.
cf. *Mesoglyphioceras granosum* (Portlock)	Fremington Pill, and Tawstock.
22. This paper (p. 212).	
Phillipsia leei Woodward.	Hole Lake Farm Quarry, Bampton.
23. Prentice, J. E. & Thomas, J. M. (1960 : 7).	Above Bampton Limestones.
Neoglyphioceras spirale (Phillips). cf. *Mesoglyphioceras granosum* (Portlock) *Dimorphoceras kathleeni* Moore *Sudeticeras splendens* (Bisat)	
24. This paper (p.212).	
Neoglyphioceras spirale Phillips	Whipcott Quarry, Westleigh.
Phillipsia leei Woodward	Whipcott Quarry, Westleigh.


British Goniatite Zones
FREMINGTON
(Prentice, J.E 1960)
BARNSTAPLE
(Prentice, J.E 1960, & unpublished)
SWIMBRIDGE
(Unpublished)
SOUTH MOLTON
(Unpublished)
BRUSHFORD
(Swarbrick, EE '62)
BAMPTON
(Swarbrick, EE '62, & Thomas, J.M '65)
WESTLEIGH
(Thomas, J.M '65)
German Goniatite Zones
P2a
P1d
P1c
P1b
P1a
B2
B1
I
Limekiln Beds
•20
•12 P
•11
Chert Beds (Fremington facies)
Pilton Beds
•1
D
C
Black Shale Formation
•21
P
Chert Beds (Codden Hill Facies)
Hearson Hill Mudstone
Combe Wood Chert
Bydown Chert
▾5
▾4
•3
Basement Formation
•2
Pilton Beds
Black Shale Formation
Bestridge Limestone
P
Smalldon Limestone
High Down Chert
•6
Basement Formation
Pilton Beds
Black Shale Formation
P
Whitehill Limestone
Black Shale Formation
Chert Formation - Brushford Member
Hele Manor Chert
Kents Hill Chert
Hulverton Hill Chert
•14
•13
•7
Basement Formation
Pilton Beds
Giffords Beds
•23
Chert Formation - Bampton Member
Baileys Beds (-U Bampton Limestone, JMT -Bampton Limestone, EES)
Kersdown Beds (-M Bampton Chert, JMT -Bampton Chert, EES)
•10
▾9
▾8
Basement Formation (EES)
Hayne Beech Beds (JMT)
Daddiscombe Beds (JMT)
Pilton Beds
▾24
•19
•18
•17
•16
•15
Upper Westleigh Limestone
Lower Westleigh Limestone
IIIβ
IIIα
II
I

•20 – Goniatite horizon ▾4 – Trilobite horizon P – Posidonia

That the species may have entered the area prior to this is indicated by its occurrence in white chert at Ideford, Devon, and in the upper part of the Bailey's Beds (Thomas 1962) at Bampton.

The correlation of these faunas with their contemporaries in the rest of the British Isles and in northern Europe presents some problems. The *M.* aff. *laticampa* locality is within 2 kilometres of the railway-cutting from which *Pericyclus* aff. *homoceratoides* is recorded by Butcher & Hodson (1960 : 76) and the latter horizon may not be very far below the base of the Chert Formation. Nevertheless this must mean that the Chert Formation begins in zone II, and a solid, but decayed, pericyclid found with *M.* aff. *laticampa* supports this correlation. The *Spatulina* fauna has been equated (Prentice 1960) with the top of zone II, a correlation confirmed by the occurrence of *M.* cf. *brevispina.* There is no doubt that this is succeeded immediately by the *Phillibole coddonensis* fauna. *P. coddonensis* is closely related to *Phillibole culmica* R. & E. Richter, and with *Ph. aprathensis* is known only from the Zone IIIβ of Germany. It seems almost certain that in the British Isles these two species extend down into the equivalents of Zone IIIα. At Warrenshill Quarry, Bampton *P. coddonensis* is found, less than a foot above a bed with *Liobole glabra,* with no sign of a stratigraphical break between. In the Brushford area, the pale cherts (Kents Hill Chert) are succeeded by beds containing $P_{1\beta}$ (i.e. Zone IIIα) goniatites (Butcher & Hodson 1960). In the north of England a form related to *P. aprathensis* characterized the B_2 zone (Calver & Ramsbottom 1962), which certainly lies below the $P_{1\alpha}$ (IIIα) zone, and which includes in its fauna *Entogonites grimmeri* Kittle, whose type material comes from Zone IIδ in Sauerland (Schmidt 1942 : 49). The occurrence of *Bollandites* cf. *castletonense,* in the Kersdown Beds (Thomas 1962) a typical B_2 zone form in the north of England, further links these *Phillibole* faunas with zones B_2 and IIIα.

The age of the *Phillipsia leei* fauna is less equivocal, as it is associated with the "*spiralis* band" lying at the P_1—P_2 junction, or in the sub-zone of $III_{\beta 7}$ (see above and Prentice 1960). The finding of a specimen of this species at a precisely similar horizon in Sauerland suggests that the fauna may be of zonal significance.

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PLATE 1

Phillipsia leei (Woodward)

All specimens from Lee Collection, British Museum (Nat. Hist.).

Posidonia shales, Waddon Barton Lane, nr. Chudleigh, N. Devon.

FIG. 1. Lectotype. In. 58281. Dorsal view of outer shell-lamina. ×4·8.

FIG. 2. Paratype. In. 58280. Ventral view of inside of outer shell lamina. ×4·8.

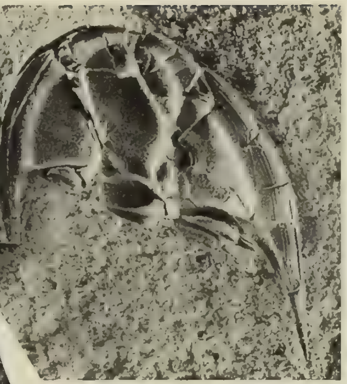
FIG. 3. Paratype. In. 58280. Counterpart of above. ×4·8.

FIG. 4. In. 58283. Mould of ventral side of free-cheek and interior of ventral doublure. ×5·2.

FIG. 5. In. 58283. Counterpart of above: ventral view of outer shell-lamina. ×5·2.

FIG. 6. Paratype. In. 58283. Internal mould of pygidium and ventral surface of doublure. ×4·8.

FIG. 7. In. 55935. Internal mould of pygidium, showing attachment scars of pygidial muscles. ×4·7.



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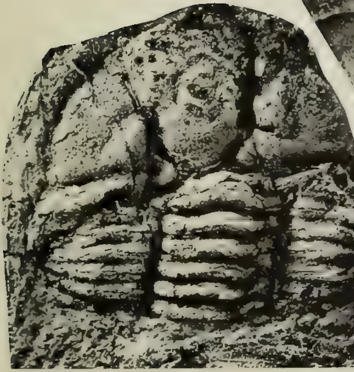

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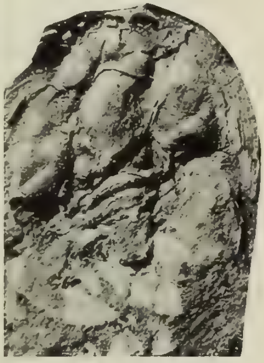

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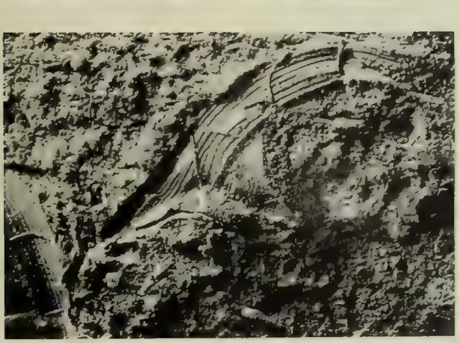

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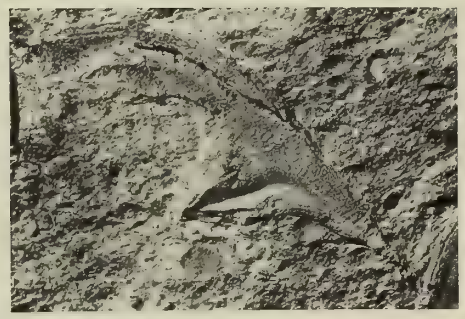

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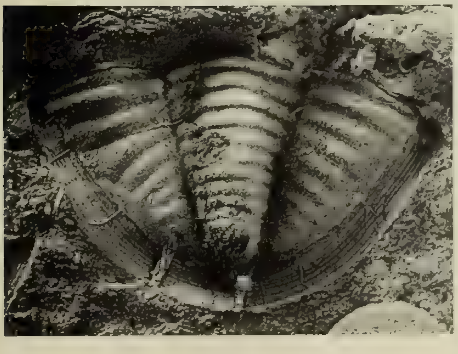

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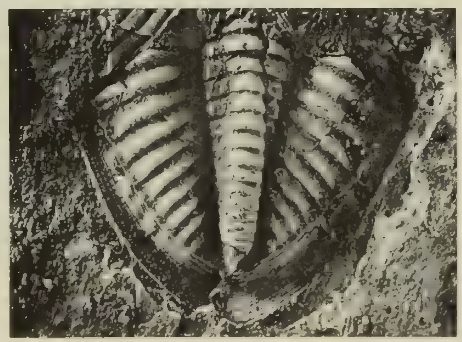

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PLATE 2

FIG. 1. ***Cyrtosymbole (Macrobole)*** cf. ***brevispina*** Osmólska. BMNH. I. 3223. Chert Formation, Park Gate Quarry, Tawstock, N. Devon. ×6·1.

FIG. 2. ***Cyrtosymbole (Macrobole)*** cf. ***brevispina*** Osmólska. BMNH. It. 444. Chert Formation, Park Gate Quarry, Tawstock, N. Devon. ×6·2.

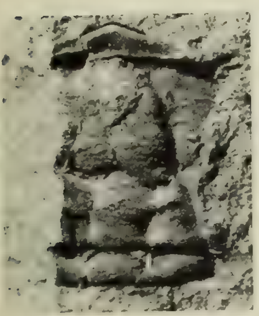
FIG. 3. ***Cyrtosymbole (Macrobole)*** aff. ***laticampa*** Osmólska. BMNH. It. 1445a, b. Chert Formation, Claypit Coverts, West Buckland, N. Devon. ×5·1.

FIG. 4. ***Typhloproetus cephalispina*** sp. nov. Holotype, BMNH. It. 1432. Bed 18, Chert Formation, Warrenshill Quarry, Bampton, N. Devon. ×3·8.

FIG. 5. ***Cyrtosymbole (Macrobole)*** aff. ***laticampa*** Osmólska. BMNH. It. 1432. Chert Formation, Claypit Coverts, West Buckland, N. Devon. ×2·8.

FIG. 6. ***Typhloproetus cephalispina*** sp. nov. BMNH. It. 1443d. Bed 18, Chert Formation, Warrenshill Quarry, Bampton, N. Devon. ×8.

FIG. 7. ***Cyrtosymbole (Waribole)? chudleighensis*** sp. nov. M.R. House collection 1100 BMNH. It. 1433. Pit L, " Posidonia " shales, N.E. of Mount Pleasant, Chudleigh, S. Devon. ×13.



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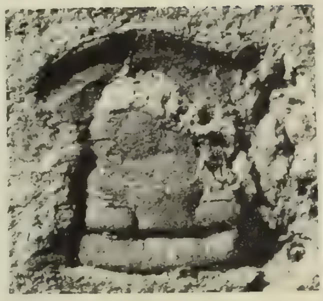

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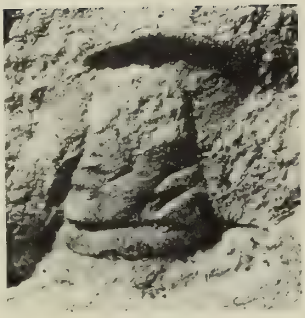

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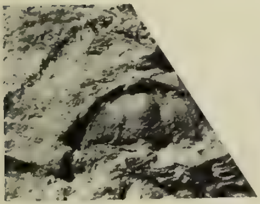

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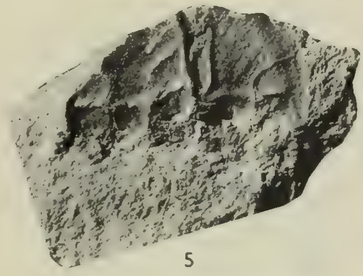

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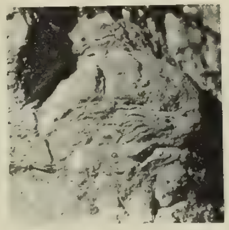

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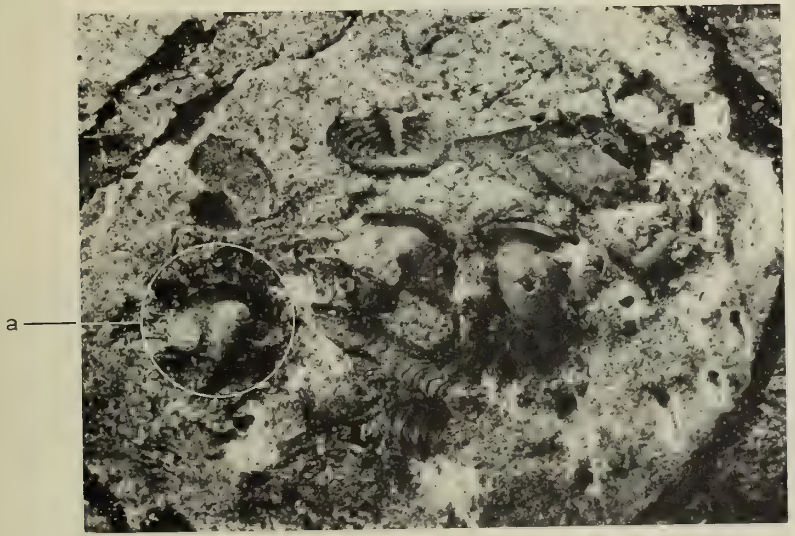

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PLATE 3

Phillibole coddenensis (Woodward)

FIG. 1. Meraspid stage. BMNH. In. 22892. Dorsal view of inner shell lamina. Wheelton Hind collection, Codden Hill. ×6·5.

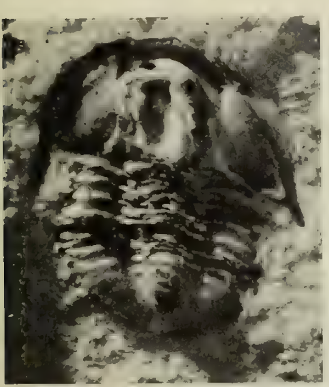
FIG. 2. Counterpart of above ; ventral view of outer shell lamina. ×6·5.

FIG. 3. Lectotype, Woodward (1902, pl. 20, fig. 8). BMNH. I. 4560. Dorsal view of inner shell lamina. Codden Hill Beds, Combe Quarry, Barnstaple. ×6·5.

FIG. 4. BMNH. I. 4565. A. Coomaraswamy collection. Dorsal view of inner shell laminae. Low Culm Measures, Coombe Wood, nr. Barnstaple. ×6·5.

FIG. 5. Syntype, figured Woodward (1902, pl. 20, fig. 9). BMNH. I. 4561. Dorsal view of inner shell lamina. ×6·2.

Specimens uncoated.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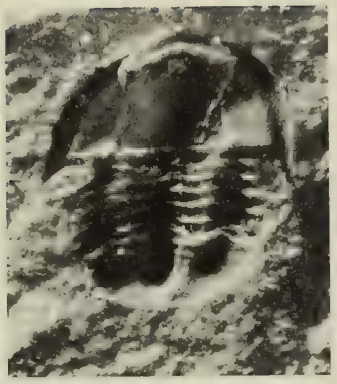
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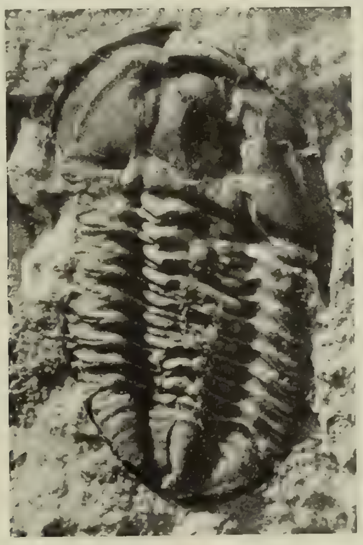
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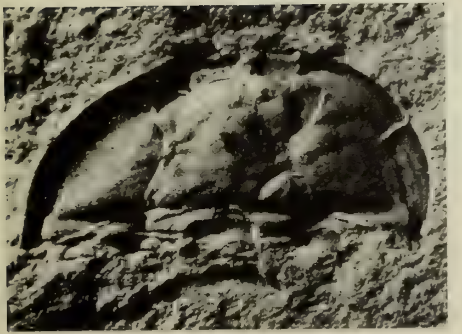
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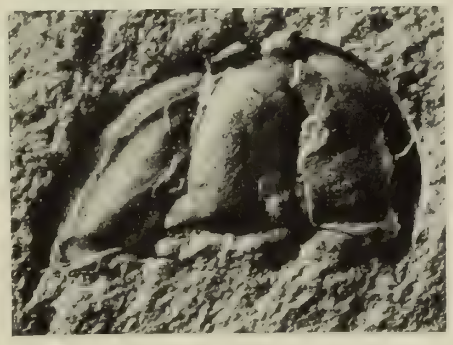
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PLATE 4

Phillibole polleni (Woodward)

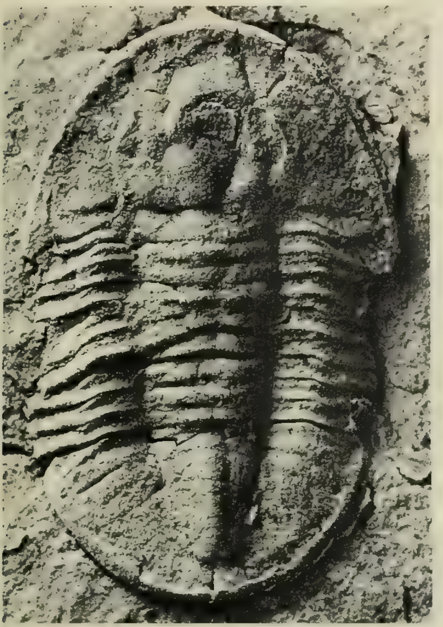
All from banks of the River Hodder near Stoneyhurst, Lancs.

Fig. 1. Lectotype, BMNH. It. 371*a*. External view of dorsal shield. Figured Woodward (1894, pl. 14, fig. 9). ×3·3.

Fig. 2. Counterpart of above. BMNH. It. 371*b*. External mould of dorsal shield. ×3·1.

Fig. 3. BMNH. It. 372. External view of dorsal shield. Figured Woodward (1894, pl. 14, fig. 10). ×3·6.

Fig. 4. BMNH. It. 373. Internal view of outer shell lamina of free cheek. Figured Woodward (1894, pl. 14, fig. 11). ×6·2.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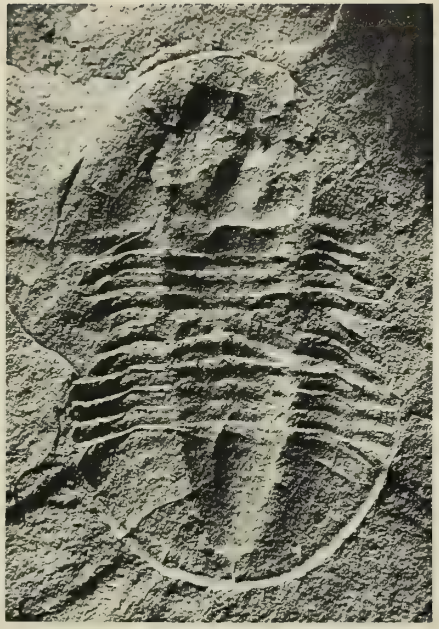
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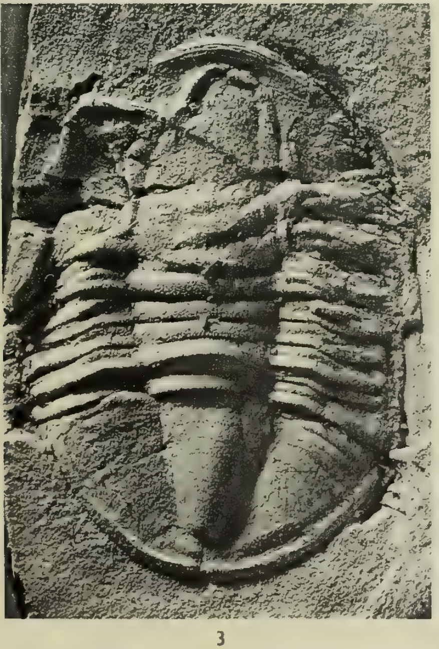
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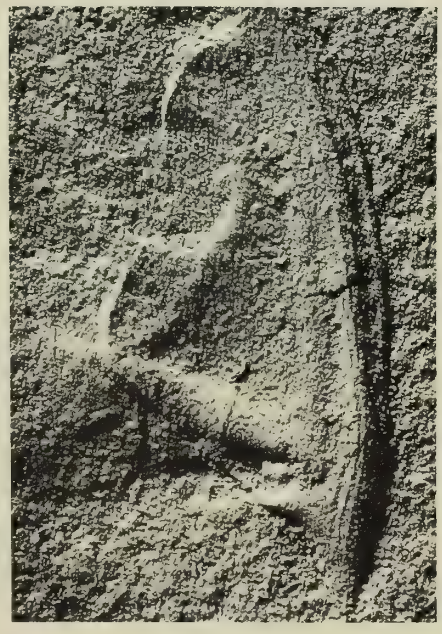
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PLATE 5

Liobole glabra (Holzapfel)

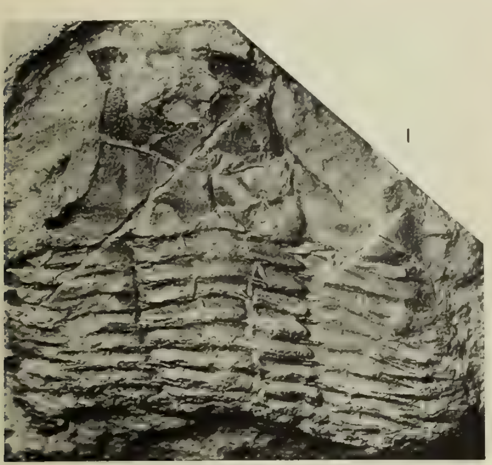
FIG. 1. BMNH. It. 1436. Chert Formation, Park Gate Quarry, Tawstock, N. Devon. × 2·4.

FIG. 2. BMNH. It. 1438. Chert Formation, Bed 15, Warrenshill Quarry, Bampton, N. Devon. × 2·3.

FIG. 3. BMNH. It. 1437. Chert Formation, Park Gate Quarry, Tawstock, N. Devon. × 3·1.

FIG. 4. N.D.A. 822. Chert Formation, Templeton Quarry, Tawstock, N. Devon. × 1·5.

FIG. 5. BMNH. It. 381. Chert Formation, Codden Hill, N. Devon. × 5·3.



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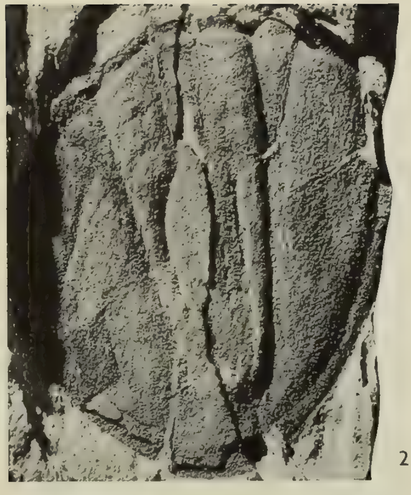

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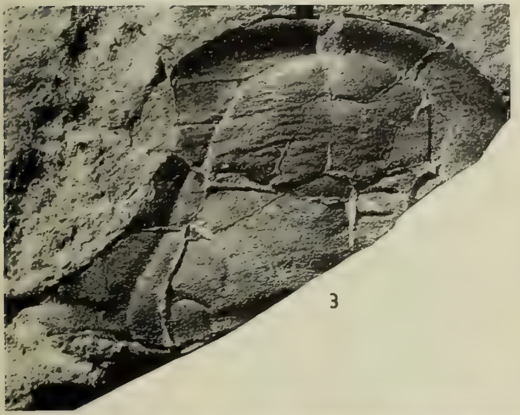

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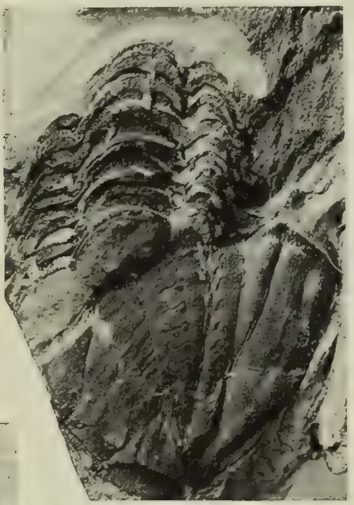

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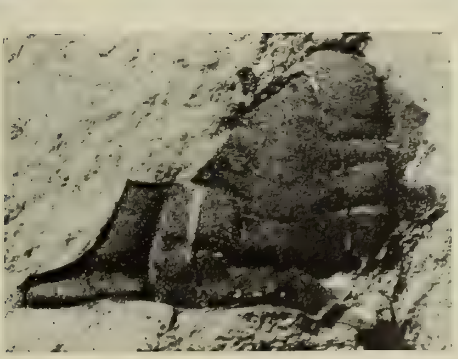

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PLATE 6

Spatulina longispina sp. nov.

Fig. 1. Holotype. BMNH. It. 1440*a*. Internal mould of carapace with inner lamina adhering. Bed X, Chert Formation, Park Gate Quarry, Tawstock. ×3·1.

Fig. 2. Counterpart of holotype. BMNH. It. 1440*b*. External mould of carapace with outer lamina adhering. Bed X, Chert Formation, Park Gate Quarry, Tawstock. ×3·1.

Fig. 3. Internal mould of pygidium with inner lamina adhering. BMNH. It. 1441. Bed X, Chert Formation, Park Gate Quarry, Tawstock. ×2·7.

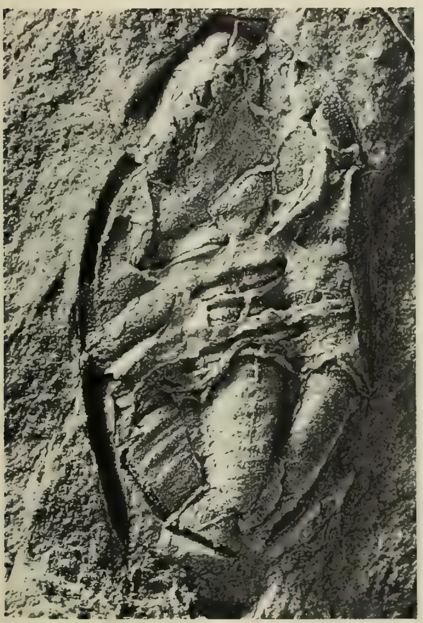
Fig. 4. Internal mould of free cheek. BMNH. It. 1441. Bed X, Chert Formation, Park Gate Quarry, Tawstock. ×4·4.

Spatulina spatulata (Woodward)

Fig. 5. Internal mould of cephalon, with inner lamina adhering. (KCL. t. 173). Chert Formation, Park Gate Quarry, Tawstock. ×4·7.

Fig. 6. External mould of cephalon, with outer lamina adhering. (KCL. t. 172). Chert Formation, Park Gate Quarry, Tawstock. ×4·3.

PLATE 6



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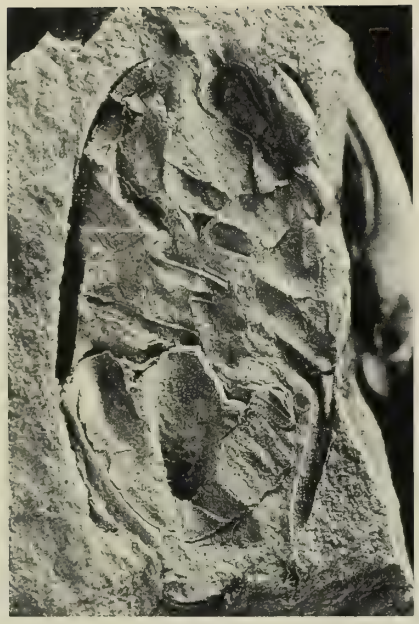

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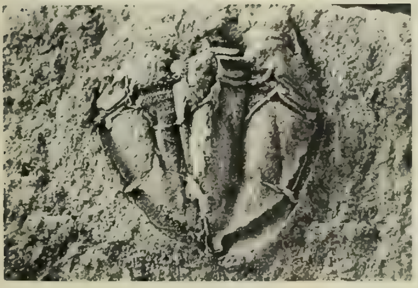

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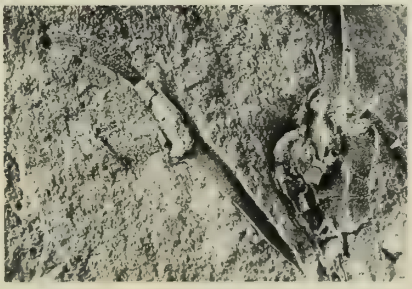

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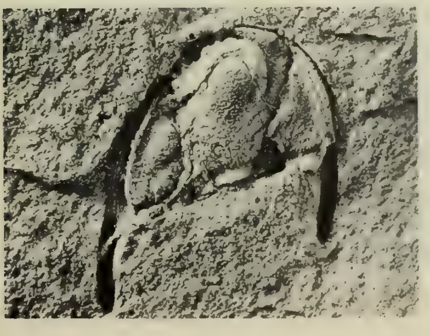

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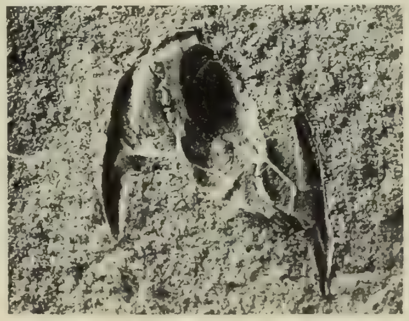

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PLATE 7

Diacoryphe? vandergrachtii (Woodward)

FIG. 1. Lectotype. BMNH. It. 1446. Banks of R. Hodder, near Stoneyhurst, Lancashire. ×4·7.

FIG. 2. Syntype. BMNH. It. 1447. Banks of R. Hodder, near Stoneyhurst, Lancashire. ×5·0.

FIG. 3. Syntype. BMNH. It. 1448. Banks of R. Hodder, near Stoneyhurst, Lancashire. ×10.

FIG. 4. Same as figs. 2, 3. BMNH. It. 1449. ×10.

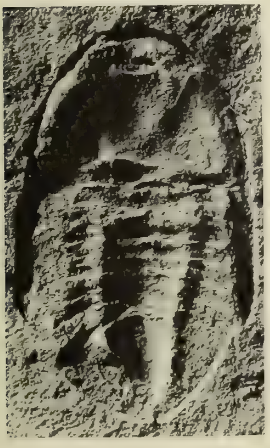
FIG. 5. Same as figs. 2, 3. BMNH. It. 1450. ×10.

Phillibole aprathensis R. & E. Richter

FIG. 6. BMNH. It. 1434. Chert Formation, loose block above Warrenshill Copse, Bampton, N. Devon. ×3.

FIGS. 7, 8. BMNH. It. 1435. Bampton Limestone Group, Little Holwell Quarry, N. of Bampton, N. Devon. ×6·5.

FIG. 9. BMNH. I. 4563. Chert Formation, Hannaford Quarry, Barnstaple, N. Devon. ×4·7.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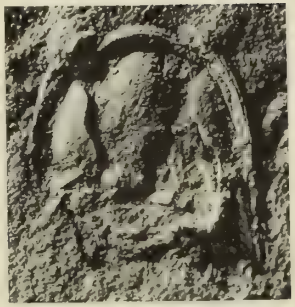
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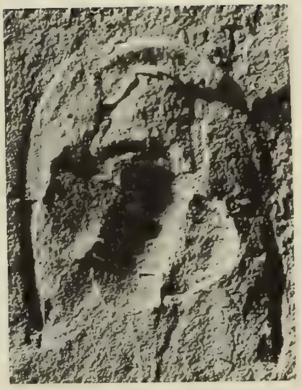
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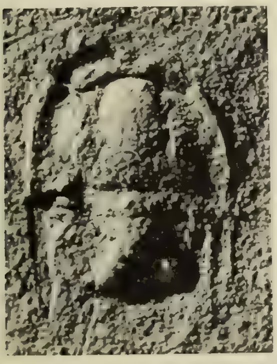
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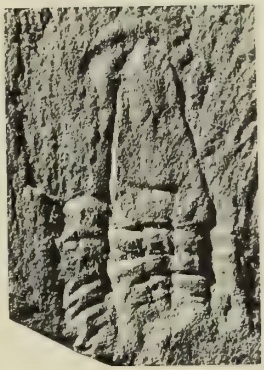
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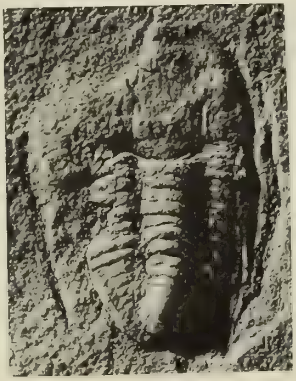
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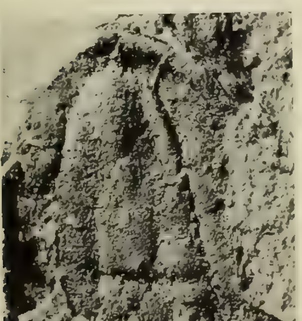
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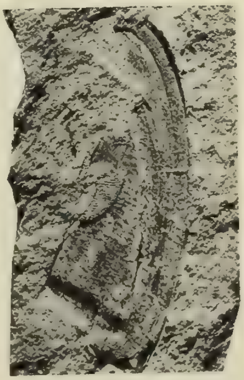
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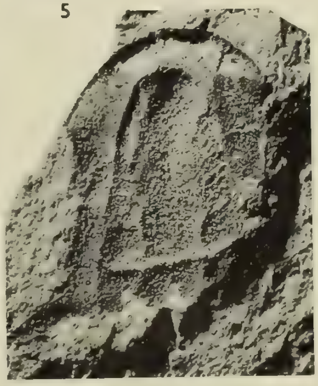
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FOSSIL MAMMALS OF AFRICA
No. 22

PELOROVIS OLDOWAYENSIS RECK, AN EXTINCT BOVID FROM EAST AFRICA

A. W. GENTRY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 14 No. 7
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BY

ALAN WILLIAM GENTRY, D.Phil.

(Centre for Prehistory and Palaeontology, Nairobi)

Pp. 243–299; 6 *Plates;* 40 *Text-figures*

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FOSSIL MAMMALS OF AFRICA
No. 22

PELOROVIS OLDOWAYENSIS RECK, AN EXTINCT BOVID FROM EAST AFRICA

By ALAN WILLIAM GENTRY

SYNOPSIS

New material of *Pelorovis oldowayensis* Reck from the upper part of Bed II at Olduvai shows that this animal is not a member of the Caprinae, but belongs instead to the Bovini and is related to the African buffalo *Syncerus* Hodgson. Material used to describe *Bularchus arok* Hopwood in 1936 is found to be assignable to *Pelorovis oldowayensis*. There is possible evidence for a second Bovine species in Bed II.

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I INTRODUCTION

In 1952 and in several subsequent years Dr. & Mrs. L. S. B. Leakey excavated at site BK II in Olduvai Gorge, a site which they had first located in 1935 and which is now known to lie near the top of Bed II. It consisted of a former land surface covered with sands and with extensive clay deposits above the sand, the land surface being littered with large numbers of splintered bones, as well as with stone tools and waste flakes of an evolved Oldowan culture. Adjoining the former land surface was a clay-filled gully in which more completely preserved animal remains including some articulated limb bones were found. Leakey (1954) believes that the men who used the land surface drove their prey into the mire of the gully and then dragged them out to be eaten, but that occasionally the larger animals had to be left behind.

From BK II were excavated a complete skull and many skull fragments of the large Bovid *Pelorovis*, also many limb bones and vertebrae among which the best preserved set of limb bones was known to have come from the same individual as the complete skull.

Remains of *Pelorovis* had first been recovered from Olduvai by the German expedition of 1913, and described as the single species *P. oldowayensis* by Reck (1925, 1928).

The holotype in Berlin is somewhat weathered and consists of the back part of a skull with its horn cores ; since the front of the skull is missing no teeth were available for Reck to work on. In his 1928 article, kindly translated for me by Mr. & Mrs. G. J. Warren, Reck noted that possible similarities to previously described fossils were few, but on the basis of horn core characters he made comparisons with various Caprines, and only briefly considered the possibility of relationship with other Bovidae such as the African buffalo *Syncerus*, or the Alcelaphini. He finally chose the sheep as being least far phylogenetically from *Pelorovis*, but was aware that the East African animal could have evolved its horn shape in isolation from other known living or fossil sheep. In fact we can now be certain, with more complete material and particularly from features of the teeth, that *Pelorovis* is not any kind of Caprine.

In the following diagnosis and expanded definition the skull is imagined as having its tooth row horizontal.

Genus ***PELOROVIS*** Reck

Type species. *Pelorovis oldowayensis* Reck, 1928.

Generic characters. As for the species.

Pelorovis oldowayensis Reck

1928 *Pelorovis oldowayensis* Reck : 57, pls. 1, 2, text-fig. 1.
1936 *Bularchus arok* Hopwood : 639.

Holotype. Back part of a skull with horn cores, in the Institut für Paläontologie und Museum der Math.-Naturwissenschaftlichen Fakultät der Humboldt-Universität, Berlin.

Referred material. A complete skull numbered Pel 1 ; horn cores and skull pieces numbered Pel 2 to Pel 23 ; an unnumbered frontlet and a left horn core ; teeth, limb bones and vertebrae as listed at various places in the text. This material is in the National Museum of Tanzania, Dar es Salaam, and a cast of the complete skull is in the British Museum (Natural History), London. Also in the British Museum (Natural History) is a frontlet with horn cores M.14947, a frontlet with left horn core M.14948, a horn core tip M.14949, and paired mandibular rami M.15856 ; all this material had been assigned to *Bularchus arok*. Also in London are teeth numbered M.25676–81, M.25688 and M.25692.

Horizon. The holotype is of unknown provenance within Olduvai Gorge ; most of the remains in Dar es Salaam are from site BK II, but there are also some from SHK and other sites in the upper part of Bed II. M.14947–48 were originally supposed to have come from Bed IV, but they are now believed to have come from Bed II (see p. 290). M.15856, M.25676–81, M.25688 and M.25692 are from Kanjera, a site which has usually been taken to be equivalent to Bed IV at Olduvai.

Age. Middle Pleistocene.

Diagnosis. A large Bovid with long curved horn cores without keels, horn cores inserted close together and so far posteriorly on the skull that they overhang the occipital surface. The face is long, the tooth row is placed anteriorly, and the median indentation at the back of the palate has its anterior edge further forwards than the lateral ones. Teeth moderately hypsodont, but have only small basal pillars, and their occlusal pattern is not advanced. The anterior part of P_4 has a medial wall.

DEFINITION. The preceding diagnosis selected the most noticeable characters of the skull; in this expanded definition are listed all those characters which I have found useful in comparing *P. oldowayensis* with some other Bovidae.

A large Bovid with a long and low skull. Its massive horn cores are slightly compressed dorso-ventrally (with the skull in a horizontal position) and without keels or transverse ridges; they arise close together, well behind the orbits and partly behind the occipital surface as well, then they pass successively backwards and outwards, then outwards and perhaps slightly downwards, then forwards and slightly or markedly upwards as well. When it is at all evident, the spiralization is therefore clockwise in the right horn from the base upwards. The horn cores taper gently from base to tip, sometimes a deep longitudinal groove runs along their back outside curve. Females have shorter and more sharply curved horns than the males. The horn cores and frontals are hollowed.

The skull is about as wide at the orbits as across the occipital surface; the frontals curve slightly downwards in lateral view as they pass forwards over the orbits. The orbits are small (probably an allometric effect) and the orbital rims project only slightly. Supraorbital foramina are found above the back part of the orbits or a short distance behind them in longitudinally extended supraorbital pits. Behind the orbits is a long temporal fossa to house the coronoid process of the lower jaw and its attached musculature. The nasals are rather domed transversely, and they are widest just behind the point where their front part loses contact with the maxillae; their central anterior flanges are pronounced and there are no lateral anterior flanges. The back of the nasals probably lies above the front half of the orbits. There is no ethmoidal fissure nor a localized preorbital fossa. The anterior part of the lower edge of the zygomatic arch passes forwards well below the orbits. The infraorbital foramen lies above or in front of P^2. The palatal fissures of the premaxillae appear to have been rather small; the premaxillae become narrower as they rise, and have little or no contact with the nasals. The tooth row is set rather anteriorly, and the median indentation at the back of the palate passes further forwards than the lateral ones. The vomer is not fused with the back of the palate. At the top of the occipital surface is a deep inverted triangular depression, the mastoid exposure of the periotic is entirely on the occipital surface, and the occipital condyles are wide. The top edge of the foramen magnum is not so posterior relative to the condyles as in *Oryx*. The anterior tuberosities of the basioccipital are sufficiently close together to give the bone a triangular shape; they are large and have poor longitudinal ridges extending behind them; there is a poor longitudinal groove along the centre of the basioccipital; and the bone is not transversely constricted across its middle. The foramina ovales are small and situated just in front of the level of the anterior tuberosities. There is an indentation in the sides of the squamosal shelf immediately in front of the mastoid. The auditory bulla is a little compressed from side to side and appears to be but little inflated. The tips of the paraoccipital processes are not noticeably turned forwards.

The teeth are moderately hypsodont ; their enamel surfaces, having many tiny longitudinal striations, may be described as rugose. The upper molars have wide and quadrate occlusal surfaces ; basal pillars are present but not strongly developed ; the walls of the central cavities of the teeth do not have a complex outline ; the styles are not strongly developed ; the outward bowings of the walls between the styles are neither localized nor strongly developed ; and cement is present. The mandible is deep below the teeth ; the anterior edge of the coronoid process is only slightly curved backwards (this is correlated with the relatively anterior position of the upper tooth row) ; and the anterior part of P_4 has a medial wall, thereby closing off a central valley on the tooth.

The great trochanter of the femur is tall with a slanted antero-dorsal edge ; there is a slight indentation between the great trochanter and the articular head in anterior view and the top edge of the articular head is a little slanted in anterior view ; the articular head is not very narrowed in its lateral part in dorsal view ; distally the lateral condyle is not sharply pointed anteriorly ; and the patellar fossa is wide. On the tibia there is no middle patellar groove at the top of the cnemial crest ; the lateral facet on the top articular surface is without an upturned lateral edge ; and distally the medial malleolus exceeds the central anterior flange in length. On the astragalus there is a deeply incised facet at the back of the medial side for the naviculo-cuboid ; the ridge for the astragalo-metatarsal ligament on the medial side is present ; this ridge is at the same level or slightly lower than the ridge for articulation with the medial malleolus of the tibia ; the top of the back of the medial side of the astragalus does not project behind or away from the main mass of the bone. The naviculo-cuboid is not deep ; and the back edge of its medial wall is fairly straight. The metapodials are not antero-posteriorly compressed ; and they possess distal anterior and posterior foramina. The articular facets at the top of the metatarsal are almost flat.

On the scapula the tuber scapulae is set above the anterior edge of the glenoid facet ; the lateral side of the glenoid facet in ventral view is slightly indented ; and the area for the origin of the teres minor extends forwards to the base of the spine. The lateral tuberosity of the humerus is low ; its posterior eminence is small and not antero-posteriorly long ; the infraspinatus insertion is longer than it is deep ; the front of the infraspinatus insertion is level with the front edge of the lateral side of the bone ; the bicipital groove is wide ; distally there is a coronoid fossa ; and the medial condyle is tall. The radius is rather long relative to the humerus for a Bovid the size of *Pelorovis*. On the ulna the area for the origin of the flexor carpi ulnaris extends near to the top of the bone, i.e. the roughened area at the top of the olecranon is smaller. On the radius the medial edge of the medial facet on the top articular surface does not project as a rim ; the postero-medial part of the medial facet is not greatly expanded ; the lateral facet is antero-posteriorly long ; the lateral tubercle is moderately sized ; the axis is not swollen at its distal end in lateral view ; and the ridge between the posterior surfaces of the scaphoid and lunate facets is slanted and not sharply marked. The carpal bones are antero-posteriorly long and not tall. The tubercle towards the front of the upper facet of the scaphoid is little pronounced ; and the lower edge of the scaphoid is little indented in medial view. Because of the length of the lunate its ventral projection where it passes behind the unciform is rather forwardly sited; the back edge is not very pointed in medial view; and the more posterior lower parts of the lateral side project little in dorsal view.

The cervical vertebrae are transversely wide and antero-posteriorly short; with neural spines not slanted forwards. The hollows on the ventral surface of the atlas are deep. The vertebrarterial foramina on the axis are small. The anterior and posterior openings of the foramen transversarium on the third cervical are close to the front and back ends of the centrum; and the transverse processes of this vertebra are already separated from their ventral flanges.

REMARKS. It is clear that *Pelorovis* cannot belong to the Caprinae, as can be seen from the skull characters alone. Its skull is relatively lower in side view than in Caprinae, its horn cores are set far behind the orbits and there is a temporal fossa, the premaxillae are not reduced as in some Caprine tribes, the anterior tuberosities of the basioccipital are not set very widely apart, its upper molar teeth are wide, they have basal pillars, they have no tendency towards exaggerated styles on the lateral walls, and there is not a pronounced reduction in length of the premolar row. The purpose of this paper is to suggest an alternative relationship for *Pelorovis*.

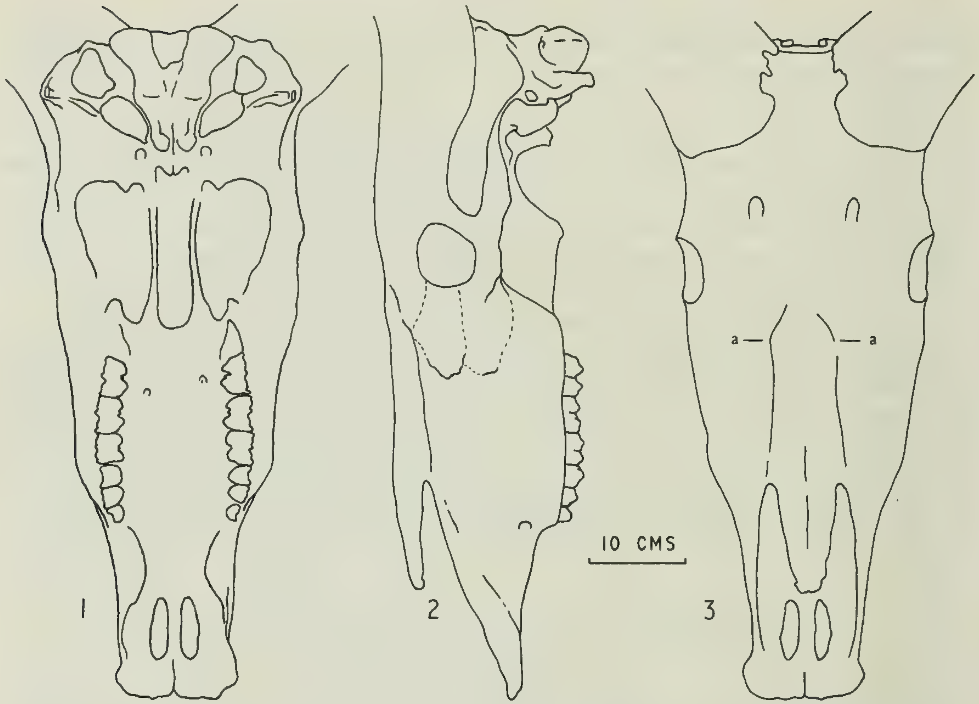
II DESCRIPTION OF NEW MATERIAL OF *PELOROVIS*

Skulls and horn cores

The complete skull

The complete skull of *Pelorovis oldowayensis* (Pls. 1, 2, 6) has been distorted in various ways—the tips of the premaxillae have been thrust upwards close to the nasals, the bones on the left side of the face have become separated, and the right P^2 and most of the left premolar row are missing. Enough of the skull has been preserved to suggest that drawings of how it might have appeared in life would be feasible, and the three resulting reconstructions are shown as Text-figs. 1–3.

Most of the characters mentioned in the definition can be seen on the complete skull. Its horn cores are not large in relation to the size of the skull; the length of the right one along its back edge is only 116 cm. which may be compared with 153 cm. for the two 1957 horn cores numbered Pel 7 and Pel 8. The short length and the sharp radius of curvature which reduces the span of these horn cores suggest that the animal was a female. The sharpness of the curvature of the horn cores precludes the possibility of them later growing to a size comparable with that of Pel 7, and the teeth show that the animal was already fully adult. Another pair of horn cores numbered Pel 18 and Pel 19 are a little smaller than those of the complete skull, otherwise the known horn cores are intermediate in size between those of the complete skull and Pel 7, without sign of a sharp distinction of males from females. In so far as the curvature of the horn cores in three planes involves spiralization, the direction of the spiralization is clockwise from the base of the right horn core. Nothing of interest concerning the horn cores can be added to Reck's (1928) detailed description of the Berlin specimen.



FIGS. 1–3. Reconstructions of skull of *Pelorovis oldowayensis*. The reconstructions are based on the complete skull Pel 1 for the pre-orbital regions, and on specimen Pel 2 in conjunction with Pel 1 for the post-orbital regions. 1, ventral view; 2, lateral view showing sutures of lachrymal and jugal; 3, dorsal view.

The supraorbital foramina cannot easily be seen on the skull; they lie above the level of the back edge of the orbits or very slightly behind them, and are not widely separated from one another. On the left side there is a very small foramen just in front of the position of the main supraorbital foramen. A narrow and shallow longitudinal furrow runs along the bone surface in front of the supraorbital foramina on both sides almost as far as the level of the back of the nasals. The anterior parts of the nasals are transversely domed, and the downflanged lateral parts of the nasals anteriorly are fused with the maxilla as often happens in large Bovidae. Although there is no localized preorbital fossa, the whole region of the face in front of the orbits and on either side of the nasals has a hollowed surface. Towards the back of the left nasal a piece of what is presumably the lachrymal rises up and shows the beginning of the posterior narrowing of the nasal; the back of the nasals is not otherwise indicated. On the left side of the face part of the suture marking the maxilla-lachrymal boundary can be seen, and lower down a more doubtful indication which, if it is a suture at all, marks part of the maxilla-jugal boundary; there is nothing worthy of comment in the position of these sutures, and they are shown in Text-fig. 2.

The lower part of the occipital surface is at an angle of 90° to the plane of the top of the skull, and two low rounded ridges run up the occipital to reach the sides of the inverted triangular depression. The paraoccipital processes have been broken off. The basioccipital has both its anterior tuberosities complete. A small basal pillar can be seen on the left M^2 and somewhat larger ones on both M^3s ; a good deal of cement remains around the basal pillars.

The lower jaws of this animal (Pl. 6), which were found in position on the underlying skull, are undistorted. All teeth are present except the right P_2, but the left P_2 has been worn very low. The basal pillars on M_1 and M_2 have been nearly worn away, but that on M_3 is still present. The front cavity on M_1 has almost disappeared.

Remains of other skulls and horn cores

All but one of the other specimens of *Pelorovis* are of posterior parts only. The most useful of these is numbered Pel 2, and possesses the proximal parts of both horn cores with a complete but fractured occipital surface between them (Pl. 3). The left side of the top of the skull is missing, presumably because the men broke into it to get out the brain ; this had not happened to the complete skull which was found in the clay filled gully. A feature to be noted is the deep groove running along the back outside curve of the horn cores. On the right upper side of the skull is a lengthened supraorbital pit containing two foramina, the front one of which lies over the back of the orbit. The posterior upper part of the right orbit has been preserved although the rim is nowhere complete. The top of the occipital surface is evenly curved and marked by a small but sharp ridge even along those parts of its course which are overhung by the horn cores' bases ; this ridge has a more constant radius of curvature from the foramen magnum than it does in *Syncerus*. An inverted triangular depression is again seen at the top of the occipital surface. The basioccipital is present but without its anterior tuberosities ; one foramen ovale and the larger foramen rotundum can be seen, also the deep and long temporal fossae beneath the bases of the horn cores. Parts of the squamosal shelf for articulation with the condyle of the mandible are present on both sides, and the thickened base of the right paraoccipital process is present.

An unnumbered complete pair of horn cores with part of the frontals and still less of the occipital surface is shown in Pl. 2. The length of the outwardly directed part of the horn cores is greater than in the complete skull and their upward curvature is less marked.

Pel 5 is a distorted pair of horn cores with the occipital, the condyles and the basioccipital still surviving. The radius of curvature of the horn cores is quite small, and both of them have a moderately sized shallow longitudinal groove running along their back curve. The anterior tuberosities of the basioccipital are missing.

Pel 3 is a less complete skull piece than Pel 2, but it has an almost complete and undistorted temporal fossa and part of the orbital rim on the left side. The specimen thus shows well the transverse constriction of the skull behind the orbits, a feature which recalls *Bos* (in which the orbital rims are more projecting and the horn cores more widely set than in *Pelorovis*). The gap between the bases of the horn cores along the top of the frontals is narrow and appears as a deep longitudinal incision; the inference from this is that the horns of Pel 3 would have been larger and longer than those of the two skulls described above. The lack of the horn cores above their bases and of most of the right frontal allows the hollowing in the bone above the brain to be seen. The horn core cavity extends to within 4 cm. of the level of the back of the orbits, and the frontals are hollowed in front of this point, but without connection to the horn core cavity. The level to which the skull is preserved along the frontals is about the same as that to which it is preserved in Pel 2 and in the type specimen in Berlin. On the ventral surface the anterior tuberosities of the basioccipital and the paraoccipital processes are again missing. The foramina ovales are in the horizontal plane and slightly in front of the anterior tuberosities.

The skull Pel 4 has retained part of its right horn core, the occipital surface, a small part of its ventral surface and part of the temporal fossa; the anterior tuberosities of the basioccipital are missing. The triangular depression at the top of the occipital surface is less pronounced than in Pel 2.

A number of *Pelorovis* horn cores have been taken from BK and other sites in Bed II at Olduvai. One of the largest is Pel 7, a left horn core excavated in 1957 from BK, which is 153 cm. long. About 12 cm. from its base there begins a deep groove which runs along the back edge as far as about 32 cm. from the tip. A small part of the occipital surface is preserved at the horn core's base. Towards its tip the horn core is turned well upwards, and thus comes to possess detectable spiralization.

Pel 8 is a right horn core from BK II which is again 153 cm. long and with about the same degree of spiralization as Pel 7; however it may belong to a different individual from Pel 7 because of its lack of a deep longitudinal groove and because the patterning of the bony surface of the frontals at the base of the horn core seems to be different. Part of the temporal fossa and a small part of the brain cavity are also preserved.

Pel 9 is a right horn core with the excavation number 1957, BK II, 1344. Spiralization is slightly less than in Pel 7 and 8, i.e. the tip is not quite so upwardly turned and remains directed mainly forwards. A rather wide, shallow, longitudinal groove exists in its more distal parts in a position slightly dorsal to that occupied by the much longer and deeper groove mentioned in Pel 7.

A left horn core, Pel 10, of which only about 40 cm. exists, may be the partner of the complete horn core Pel 9. A further piece of this left horn core may be preserved as the tip numbered Pel 11 which has a similar shallow longitudinal groove.

Pel 12 is a right horn core which is a little smaller than those mentioned previously and is less upwardly curved towards its tip. There is no longitudinal groove along the back surface. A very small part of the frontal and of the occipital surface has survived.

Pel 13 is a left horn core without its tip; it is more sharply curved than Pel 12, and a wide shallow, longitudinal groove exists for a short distance in its more distal parts.

Pel 14 is an incomplete right horn core, rather little compressed and with some degree of spiralization. Since the core is broken off about 60 cm. above its base, the degree of spiralization is only reliably indicated by the course of the longitudinal grooving and ridging on the lower part of the core. A wide and marked but rather shallow longitudinal groove begins on the back outside curve of the horn core about 15 cm. from the base. A fragmentary right horn core, Pel 17, could come from the same individual as Pel 14.

Pel 15 is a left horn core with part of the frontal, occipital and basicranial surfaces attached, and the brain cavity itself has survived practically complete. The anterior tuberosities of the basioccipital are missing and the left foramen rotundum can be seen. The base of the right horn core is also present. The left horn core overhangs the top of the occipital as in other *Pelorovis* specimens.

Pel 16 is a much damaged fragment of a left horn core with part of the frontal remaining at the horn base.

Pel 22 is a right horn core which exists in two unconnected pieces, and shows much spiralization. Its span would have been about 69 cm., and compares with about 41 cm. for the female horn core Pel 18 (see below) and about 93 cm. for the large Pel 7.

Pel 6 is a very crushed and incomplete right horn core about 70 cm. long. It comes from site SHK II about 26 feet lower than BK II.

Except for Pel 1, all the horn cores and skull remains hitherto considered may be regarded as being either of males or of indeterminate sex. Two further horn cores agree with Pel 1 in appearing to belong to female animals, these have been numbered Pel 18 and Pel 19. They are evenly tapered along their entire length, but considerably shorter and more sharply curved than the other horn cores ; the tips are more upwardly curved than in males of comparable size. The right horn core, Pel 18, has attached to it a part of the frontal, the back of the orbit and the roof of the temporal fossa. The temporal fossa is less deeply excavated than in either of the skull pieces numbered Pel 2 and Pel 3, and this is presumably linked with the smallness of its horns. Pel 19 is very probably the same individual as Pel 18.

There are also many other fragments of distal ends or the more distal parts of horn cores assignable to *Pelorovis* ; from these broken pieces we can see that the horn cores had thickened outer shells, inside which was a central cavity becoming narrower towards the tips. At any one level of cross section the thickness of the outer shell varies, but I did not find any of the internal struts which Reck (1928) refers to and illustrates.

A well preserved basicranial piece, Pel 20, shows several interesting features. The occipital condyles, being complete and undistorted, are wide as in other *Pelorovis* remains ; the basioccipital has its anterior tuberosities with slight longitudinal ridges behind them ; the bases of the auditory bullae show them to have been rather compressed and presumably poorly inflated. Both external auditory meati can be seen. This specimen is the only one to retain complete paraoccipital processes, they are short and squat and their tips are not at all forwardly directed. Parts of the occipital surface and of both temporal fossae are also preserved, but they give no information not already available from other specimens.

There is an occipital fragment, Pel 21, possessing both condyles and part of the right temporal fossa.

Tooth remains

From a badly crushed skull, Pel 23, there have been preserved parts of both maxillae and premaxillae (Pl. 3) and of the tooth rows. The premaxilla is wide at its base but narrows rapidly as it rises ; at its top it joins the maxilla in a sutural contact with the nasals, as often happens in large Bovids. Its teeth are a little smaller than others assigned to *Pelorovis*.

A good number of fossil maxillary and mandibular pieces and isolated teeth belonging to large Bovids are present in the collections from Olduvai. Many of them have morphological characters appropriate for very large Alcelaphini, but the largest among them are clearly not Alcelaphine and must belong to *Pelorovis*. Examples of its upper teeth are distinguished from those of Alcelaphini by the fact that the whole tooth row is more or less straight and not set in an arc, by the presence of rather weakly developed basal pillars, and the relatively simple course of the enamel walls of the central cavities. They appear to be less hypsodont than the Alcelaphine teeth, although this is an awkward feature to assess except with unworn examples of both groups for comparison. Finally, the upper teeth of *Pelorovis* are wider than those of Alcelaphini. Many examples of both upper and lower *Pelorovis* teeth show rugosity of the enamel, a characteristic which is perhaps of use in binding the surrounding cement to the tooth. The largest lower teeth of Bovidae in the Olduvai collections differ from those of Alcelaphini by the presence of basal pillars. It is apparent from looking at the mandibles and lower teeth that the size of a basal pillar will change with the stage of development of its tooth. In little worn teeth the level of the top of the basal pillar may not have been reached, later the level of maximum cross section is reached, finally in much worn teeth the level of the bottom of the basal pillar is passed, and it becomes joined to the body of the tooth.

1957, SHK II, 232 (Pl. 3) is an adult right maxilla with P^4 to M^3. Its teeth are comparatively little worn, and they show the relatively simple occlusal surfaces of the teeth of even younger *Pelorovis*.

A number of isolated upper molars are mostly smaller than the M^2s in the complete skull ; they all have traces of infoldings into the central cavities but these are never very pronounced. The outline of the occlusal surfaces becomes more squared medially as the teeth are worn down.

A few pieces of large Bovid mandibular ascending rami belonging to *Pelorovis* are known : 1953, BK II, area C, 91?, can be identified by the relative lack of curvature on the anterior edge of its coronoid process. Its mandibular foramen is situated about half way between the front and the back edges. Two other condyle fragments are a right and left pair with the excavation numbers 1955, BK II, 5 and 6. The top of a left ascending ramus, 1952, BK II, 123, differs from the other mandibular remains of *Pelorovis* by the lowness of its coronoid process above the condyle ; it could perhaps have come from a younger and smaller animal.

A number of specimens of lower teeth give information additional to that available from the more worn teeth of the mandible belonging to the complete skull.

1952, BK II, 117 (Pl. 3) is a left mandibular fragment containing all of the teeth from P_4 backwards except that M_3 is without its posterior lobe. The top of the jaw is rather more concave than in older specimens. The P_4 has not been long erupted and the anterior part of its medial wall is only just closed at the top. The tops of the medial edges of the lobes on the molars rise high above the level of the tops of the intervening styles. The basal pillar is small on M_1, was probably bigger on M_2, but is not yet visible on M_3. The anterior end of the comparatively little worn M_3 has a sharply medially turned flange, but this would have become less pronounced with increasing age. Each molar has little contact with the molar immediately in front.

1952, BK II, 118 is another fragment of a left mandible, but here M_3 is the only tooth to have survived, P_3 to M_2 being broken off at their necks. M_3 has been about as much worn down as in the mandible of the complete skull. A great amount of cement has been preserved between the first and second lobes of M_3, and the first lobe has been excessively worn down on its medial side.

1952, BK II, 119 (Pl. 3) is another left mandible fragment, this time preserving at least parts of all its teeth. The adult premolar row is newly erupted, P_4 has a closed anterior part of its medial wall, there is only narrow contact between M_3 and M_2, and there is again a strong medially turned flange at the front of M_3. The front of M_2 has been pushed into the back of M_1, and since the underlying part of the jaw bone is complete and undistorted this appears to have occurred in the living individual. In addition the plane of the occlusal surface of the front of M_1 shows that 119 is a second example of an animal with a tooth deformity. This jaw comes from a younger animal than 117 and since the incomplete but little worn M_3 is exposed to its roots, one can get an impression of the hypsodonty of the species. The ramus looks as if it is less deep than the one belonging to the complete skull. The medial sides of the lobes do not rise so high in comparison with the styles as in 117, but this probably has no taxonomic significance. The level of the top of the basal pillar has not been reached by the occlusal surface of M_3, the pillar is quite large on M_2, and its condition in M_1 cannot be clearly seen.

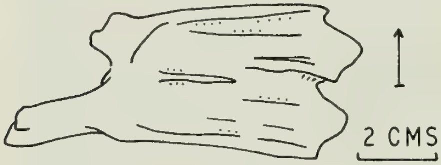
1957, BK II, 1032 is a left mandibular fragment which has M_2 and M_3 in an early state of wear, hence they are not very wide at their occlusal surfaces. The last lobe of M_3 has not been worn at all, and the central cavities of its first and second lobes are still open medially at their posterior ends. Basal pillars are not visible on either tooth, perhaps because the pillar of M_2 is hidden under cement while that of M_3 has not yet been reached.

1952, BK II, 127 is a left mandibular fragment with M_1 to M_3, the central cavity of the front lobe of M_1 having been worn away. An unnumbered specimen consists mainly of plaster around a left M_1 to M_3 in which much cement is present and the front central cavity of M_1 is again missing. 1953, BK II Extension, 79 is a right mandibular fragment with M_3 and most of M_2 in about the same state of wear as the last two pieces. An unnumbered fragment from MRC II is a piece of a left mandible with M_3, M_2 and the roots of M_1.

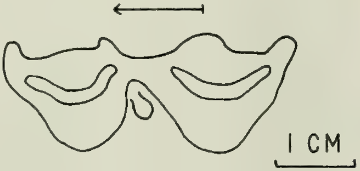
There are a good number of isolated lower teeth among which some show points of interest. Thus 1957, SHK II, 165 is a little worn right M_3 which shows anteriorly a medial flange becoming less prominent towards the base of the tooth; a basal pillar is present all the way down. 1952, BK II, 129 (Text-fig. 4) is a little worn right

M_1 or M_2 which shows well the height of these animals' teeth and in addition preserves one of its roots complete.

A lower left molar, 1953, BK II Extension, 355 (Text-fig. 5) is likely to have belonged to a *Pelorovis* yet differs from other lower molars in having less pronounced and more localized outbowings of the medial walls between the styles.



4 1952 BK II 129



5 1953 BK II EXT. 355

FIGS. 4, 5. Medial view of right lower molar 1952, BK II, 129, and occlusal view of left lower molar 1953, BK II Extension, 355. The arrows point anteriorly.

Measurements of skulls and teeth

On the complete skull—Pel 1—the following measurements, all expressed in centimetres, were taken:

Skull length from the front of the premaxilla to the back of the occipital condyles, estimated before distortion at	68·8
Skull width across the posterior side of the orbits	27·4
Distance from the front of the premaxilla to the nearest point on the orbital rim	42·4
Length of horn core along its back edge	116
Dorso-ventral diameter of horn core at a distance from its base along the back edge equal to half the maximum diameter at its base	9·7
Diameter of the horn core at 90° to above measurement	12·4
Width between the supraorbital foramina, taken between the central points of their lateral walls	11·6
Length of nasals, estimated at	31·8
Width of nasals, taken across level **a** in Text fig. 1	6·8
Distance from the front of premaxilla to rearmost point of occlusal surface of M^3, estimated before distortion at	34·9
Distance from the rearmost point of occlusal surface of M^3 to back of occipital condyles, estimated before distortion at	34·0
Occipital height from the top of foramen magnum to top of occipital crest	11·1
Skull width across mastoids immediately behind external auditory meati	27·3
Width across anterior tuberosities of basioccipital	4·9
Width across posterior tuberosities of basioccipital	8·5
Occlusal length M^1 to M^3	11·1
Occlusal length of M^2	3·75
Occlusal width of M^2	3·3
Occlusal length M_1 to M_3	11·8
Occlusal length M_2	3·5
Occlusal width M_2	2·1
Occlusal length P_2 to P_4	6·0
Occlusal length of the heavily worn P_2	1·5

Measurements on other skull pieces of *Pelorovis* were:

	Pel 2	Pel 3	Pel 4	Pel 20
Skull width at orbits . .	—	28·2	—	—
Width between supraorbital foramina	13·4	15·0	—	—
Occipital height . . .	9·9	9·7	13·2	—
Skull width at mastoids .	26·8	27·3	23·8	26·7
Width across ant. tubs. of basioccipital . . .	4·2	4·5	4·1	5·0
Width across post. tubs. of basioccipital . . .	7·8	7·7	8·3	8·7

Measurements of width of anterior and posterior tuberosities on other basioccipitals were: Pel 5, 4·3 and 8·3; Pel 15, 4·1 and 7·25.

Horn core dimensions, taken as indicated above, were:

	Dorso-ventral diameter	Diameter at 90° to the last	Length
Pel 2	9·2	13·1	—
Pel 7	11·6	13·8	153*
Pel 9	10·5	14·0	142*
Pel 12	10·6	13·6	149
Pel 18	9·6	12·6	102
Pel 5	10·4	14·1	—
Pel 6	11·1	13·3	125
Pel 4	11·3	13·9	—
Pel 14	11·7	14·3	—
Pel 15	11·0	15·4	—
Pel 22	11·1	14·0	—

* The tips of these horn cores are of plaster.

The span between the tips of Pel 6 horn cores was 184, and of Pel 7 and Pel 8 together 205.

Pel 23 had the following tooth measurements: length M^1–M^3 9·95; length M^2 3·1; width M^2 2·7; length P^2–P^4 6·05; length P^2 1·9.
The right maxilla 1957 SHK II 232 has length M^1–M^3 10·2; length M^2 3·5; width M^2 2·7.
The mandible 1952 BK II 117 has an M_2 3·9 long × 1·8 wide.
The mandible 1952 BK II 119 has length P_2–P_4 6·75; length P_2 1·8; height of M_3 from its neck to the valley on the medial side between the first and second lobes 5·9.
1957 BK II no number has an M_2 3·7 long.
The unnumbered left mandible with much plaster has an M_2 measuring 3·6 long × 2·0 wide.
A left mandible fragment 1952 BK II 127 has length M_1–M_3 11·1 and M_2 3·4 long × 2·0 wide.

A list of isolated upper molars follows, for most of which length and breadth are given: 1941 surface of Bed I F.107 3·4 × 2·45; 1952 BK II 124 3·9 long; 1952 BK II 140 3·7 × 2·4; 1952 BK II 141 is probably the same individual as 140; 1952 BK II 132?, 292 and 293 are heavily worn; 1953 BK II Extension 57 3·6 × 2·1; 1953 BK II Ext. 90; 1953 BK II Ext. 107 3·3 × 3·1; 1953 BK II Ext. 299 3·65 × 2·4; 1953 BK II Ext. 302 is probably from the same individual as 299; 1953 BK II Ext. 352 3·55 × 2·1; 1955 BK II 97 3·8 long; 1955 BK II 116 3·7 long; 1955 BK II 224 two left upper molars measuring 3·7 × 2·7 and 3·3 × 2·6; 1955 BK II 322 3·5 × 2·6; 1957 BK II 694 a fragmentary upper molar; 1957 BK II 880 3·4 × 2·6; 1957 BK II illegible number is probably the same individual as 880; 1957 SHK II 179; no number 3·6 × 2·5.

Isolated lower molars are : 1952 SHK II 668 fragmentary ; 1953 BK II area C no number M_1 or M_2 3·3 × 1·9 ; 1953 BK II Extension 58 M_1 or M_2 3·6 × 1·3 ; 1957 BK II 974 a much worn M_1 or M_2 ; 1957 SHK II 1129 M_1 or M_2 ; 1953 BK II Ext. 79 M_3 4·9 × 1·8 ; 1955 BK II 282 M_3 ; 1957 SHK II 165 M_3 4·5 long. 1952 BK II 129 (Text-fig. 4) is a right M_1 or M_2 measuring 3·75 × 1·5 ; since it is scarcely worn its height may be measured as was that of M_3 on the mandible 1952 BK II 119—the distance is 5·3. The left M_1 or M_2 1953 BK II Extension 355 is 3·6 long.

Many isolated upper premolars are assigned to *Pelorovis* : 1952 BK II 134, 142, 143, 144, 145 and 146 ; 1953 BK II Extension 86, 300 and 301 (probably from the same individual as molar 299), and 361 ; 1957 BK II 653, 692, 977, 1077, 1361? and 1461. Isolated lower premolars are 1953 BK II Extension 87 ; 1955 BK II 143 and 144.

Finally there are numbers of large incisors which probably belong to *Pelorovis*, and an unnumbered fragment of a mandible with a premolar which is not sufficiently brachyodont for a giraffid, and which is small in comparison with the size of the mandible.

Limb bones

There is from site BK II an almost complete limb bone skeleton belonging to the same individual as the complete skull of *Pelorovis* ; this skeleton can be used as a basis for description of the characters and proportions, while other fragmentary limb bones sometimes supplement this information. The largest Bovid limb bones from BK II and other Bed II sites are taken to be from *Pelorovis* because they showed no substantial morphological differences from the associated *Pelorovis* skeleton. The characters of the limb bones have already been listed in the definition of *P. oldowayensis*, and there follow here points of lesser interest. Occasional comparisons are made with the African buffalo *Syncerus caffer* because this is the largest living Bovid in Africa and because a skeleton of it was available in Nairobi.

Femur

The paired *Pelorovis* femora, 1952, BK II, 267 and 268 (Pl. 4 ; Text-figs. 12–14) from the associated skeleton are very slightly longer than the buffalo, and are at least as thin. Other femoral fossils are : 1952, BK II, 187—a right proximal end, and 1953, BK II Extension, no number—a right proximal end which is slightly smaller than those from the complete skeleton.

Tibia

The tibiae of *Pelorovis* are longer and proportionately more slender than in the buffalo. Tibial remains assigned to *Pelorovis* are:

1952, BK II, 269,	right complete, from the associated skeleton (Pl. 4)
1952, BK II, 270,	left complete, from the associated skeleton
1952, BK II, 189,	left distal end
1952, BK II, 190,	right distal end
1952, BK II, 881,	right distal end
1953, BK II Extension, 179,	right distal end
1953, BK II Extension, 421,	left distal end and part of shaft

Calcaneum

Only two calcanea, 1952, BK II, 195 (right) and an unnumbered left one, are referable to *Pelorovis*. They are longer bones than in the buffalo, as is shown in measurements. The height of the top of the astragalus facet above the base of the bone was 5·7 cm. in both the fossil 195 and the Recent buffalo specimen, but the length of the buffalo calcaneum was 11·1 and of the fossil 11·9 cm.

Astragalus

The astragali of *Pelorovis* are slightly taller and less squat than in the buffalo. Assigned specimens are:

1952, BK II, 191,	left
1952, BK II, 196,	right ; this is the largest one.
1957, BK II, 625,	right
1957, BK II, 1413,	left (Text-figs. 16–18)
1953, BK II Extension, 324,	left
1953, BK II Extension, 325,	left
1957, SHK II, 1164,	right
1959, KK II, 211,	right

An unnumbered astragalus is about the same size as these but is more squat. It is illustrated in Text-fig. 19. I think that its proportions are too different for it to belong to *P. oldowayensis*. Measurements (in cm.) of the length and breadth of the astragali in the above list are: 191, 8·5 × 5·6 ; 196, 9·2 × 5·8 ; 625, 8·5 × 5·6 ; 1413, 7·9 × 5·2 ; 324, 8·3 × 5·6 ; 211, 7·4 × 5·1 cm. The mean of the ratios of breadth as a percentage of length is 66·2, while the squat astragalus measures 7·9 × 6·2 and has a ratio of 78·5. Two astragali numbered M.12802 are in the Felix Oswald Collection at the British Museum (Natural History) ; they come from Homa Mountain and agree with *Pelorovis* in size and proportions. One would need other bones for a positive identification.

Naviculo-cuboid

Naviculo-cuboids belonging to *Pelorovis* are :

1952, BK II, 192,	right
1952, BK II, 209,	left
1955, BK II, 282,	left
1952, BK II, no number	fragmentary right
No numbers	two left (Text-figs. 22, 23)

The smaller of the two unnumbered naviculo-cuboids (Text-fig. 23) has a nearly vertical back edge of the medial wall.

Metatarsal

The metatarsal of *Pelorovis* is considerably longer than in the buffalo and proportionately more slender. A number of distal ends exist and can be identified as left or right by the slight asymmetry of the condyles—the medial side is a little smaller than the lateral side and its lowest point a little higher than the corresponding point on the lateral half. Also the lateral tendon insertion at the distal end is usually noticeably deeper than the medial one. Bones assigned to *Pelorovis* are :

1952, BK II, 275,	left complete, from the associated skeleton (Pl. 5 ; Text-figs. 24, 26)
1952, BK II, 197,	right proximal end
1953, BK II Extension, 415,	right proximal end
1957, BK II, 630,	left proximal end
1952, BK II, 220,	left distal end
1953, BK II Extension, 316,	right distal end
1953, BK II Extension, 413,	right distal end
1953, BK II Extension, 414,	left distal end
MRC II, no number,	right distal end

Scapula

The two bones assigned to *Pelorovis* are :

1952, BK II, 183,	a left stem (Text-figs. 27, 28)
1953, BK II Extension, 122,	another left stem

122 is larger and has a more pronounced muscle insertion at the back of the medial side of the stem, a character which is seen in some large Bovinae.

Humerus

Humerus specimens assigned to *Pelorovis* are :

1952, BK II, 271,	left complete, from the associated skeleton (Pl. 4)
1952, BK II, 272,	right complete, from the associated skeleton
1952, BK II, 184A,	right proximal end
1952, BK II, 185,	right proximal end
1957, BK II, 1847,	left articular head
1955, BK II, no number,	left shaft
1941, S.2, F.929,	left distal end
1952, BK II, 186,	right distal end
1952, BK II, 352,	left distal end
1953, BK II Extension, 44,	right distal end
1953, BK II Extension, 317,	right distal end
1953, BK II, no number,	right distal end

The proximal end 184A has the front of its articular head more ventrally sited than in the other specimens, but this is probably not an indicator of specific difference.

Radius

Radii assigned to *Pelorovis* are :

1952, BK II, 273,	left complete, from the associated skeleton (Pl. 4 ; Text-figs. 31, 32)
1952, BK II, 274,	right complete, from the associated skeleton
1955, BK II, 294	left, almost complete (Text-figs. 33, 35)
1952, BK II, 353,	right proximal end
1953, BK II Extension, 425,	right proximal end (Text-fig. 34)
1952, BK II, 188,	right distal end
1955, BK II, 242,	left distal end
1953, BK II Area C, no number,	right distal end, water rolled
SHK II, 25,	right distal epiphysis

SHK II, 25, for which the year of excavation is unknown, and a fragment of an axis vertebra 1957, BK II, 889 are the only known juvenile pieces of *Pelorovis*. 1955, BK II, 294 is smaller than the other radii and more swollen at its distal end in side view ; it could be a different species from *Pelorovis oldowayensis*.

Carpal bones

Only one poorly preserved right unnumbered scaphoid of *Pelorovis* is available. It is less tall and slightly longer than in the African buffalo ; such proportions are seen in all the carpal bones. There are two lunates of *Pelorovis*, one left and one right, and both of them unnumbered. A left and a right cuneiform are both unnumbered. A left and right magnum-trapezoid are both unnumbered ; the better preserved left one is antero-posteriorly longer and also broader than in the buffalo, the other one is smaller and has proportions more like *Syncerus*. There are an unnumbered left unciform and a right one numbered 1957, BK II, 1255.

Metacarpal

Metacarpals belonging to *Pelorovis* are :

1952, BK II, 277,	left complete, from the associated skeleton (Pl. 5)
1957, BK II, 1037,	left proximal and distal ends of the same bone (Text-fig. 36)
1955, BK II, 295,	left, almost complete
1955, BK II, 82,	right proximal end
No number,	poorly preserved right proximal and distal ends
1952, BK II, 199,	distal end
1952, BK II, 354,	distal end
1953, BK II, no number,	distal end
1953, BK II Extension, 52,	distal end
1953, BK II Extension, 138,	distal end
1953, BK II Extension, 170,	distal end
1955, BK II, 147,	distal end
1957, BK II, 19,	distal end
1957, BK II, 863,	distal end
1957, BK II, 1188,	distal end
1957, FC S, 367	distal end

It is not possible with metacarpal distal ends to distinguish left from right as was done with the distal ends of metatarsals. The complete metacarpal is longer than in the buffalo and rather thinner. 1957, BK II, 1037 is a larger bone than the complete metacarpal, but it cannot belong to the giraffid *Sivatherium* because the medial facet is not sufficiently flat and because of the existence of a small ridge between the medial and lateral facets. 1955, BK II, 295 is rather small and presumably came from the same individual as the radius 1955, BK II, 294.

Phalanges

Five fossil first phalanges are without numbers, one of them being from MRC II, others are numbered 1952, BK II, 202, 203 and 208, and 1941, S.1, F.837. Five second phalanges are without numbers, one of them again being from MRC II, the others are 1952, BK II, 201 and 204, 1955, BK II, 231 and 1941, S.1, F. 326. 1952, BK II, 239 and 321 are smaller bones but probably within the range of variation of the species. The length of combined first and second phalanges was greater in *Pelorovis* than in the buffalo ; for short (front) phalanges *Pelorovis* measured 11·6 cm. and two buffaloes 11·0 and 11·1, while for longer (back) ones *Pelorovis* measured 12·0 against 11·5 and 11·6 for the buffaloes.

There are six third phalanges without excavation numbers, plus 1952, BK II, 200 and 205, 1953, BK II Extension, 402, and a somewhat smaller bone 1952, BK II, 238 evidently matching the second phalanx 239.

Measurements of limb bones

Measurements of length (in cm.) were taken on the long limb bones of the associated skeleton of *Pelorovis* :

Length of femur from the lateral end of the articular head to the ventralmost level of the medial condyle	43·3
Length of tibia from the ventralmost point of the top medial facet to the tip of the bone behind the medial malleolus	43·1
Length of metatarsal from the highest point of the bone behind the medial part of the ectocuneiform facet to the articular surface on the medial side of the most projecting part of the medial condyle distally	27·5
Length of humerus from the top of the lateral tuberosity to the ventralmost point of the medial side distally	35·1
Length of radius from the medialmost point of the medial facet to the most distal point of the ridge bounding the scaphoid facet medially	35·5
Length of metacarpal from the anterior edge of the articular facet at the extensor carpi radialis insertion to the articular surface on the median side of the most projecting part of the medial condyle distally	23·8

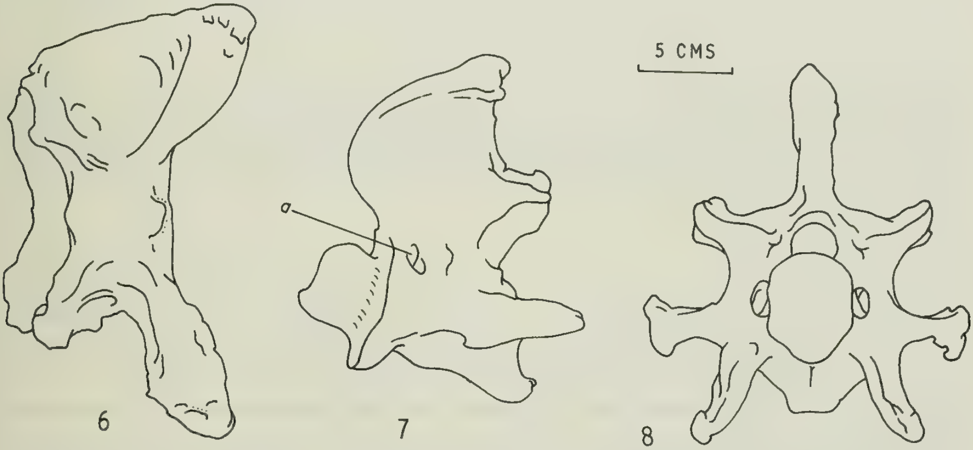
Least thicknesses of these bones were : femur, 5·23 ; tibia, 5·72 ; metatarsal, 3·90 ; humerus, 5·01 ; radius 5·44 ; metacarpal, 4·88. The left radius 1955, BK II, 294 was c.32·7 long and had a least thickness of 4·81.

Vertebrae

A great many vertebrae belonging to large Bovidae are known from BK II.

Atlas

The best preserved atlas (Text-fig. 6) belongs to a complete row of cervical vertebrae which may have belonged to the same individual as the skull to be described on p. 291. It is a wide and very short bone with large transverse processes which do not extend very far posteriorly. The sides of the bone are straight or very slightly convex.



Figs. 6–8. Three vertebrae from a complete set of cervicals. 6, atlas in ventral view ; 7, axis, in lateral view ; 8, fifth cervical in anterior view. *a* = vertebrarterial foramen.

A second and less complete atlas is similar to the first but more indented at the front of the dorsal side.

A third atlas has its transverse processes projecting less backwards, and more prominent ridges behind the ventral hollows, which may be correlated characters. Its front articular facets are less wide than in the first two atlases mentioned, and its dorsal side slightly more hollowed.

A fourth atlas has still more pronounced ridges at the back of the ventral surface than in the last one, and its front articular facets are as narrow as in that specimen. The dorsal hollowing is intermediate between that of the first two and the third atlases mentioned above. The indent at the front of the dorsal surface is as deep as in the second atlas, and the openings for the vertebrarterial and alar foramina are well separated in an elongated common fossa. It is conceivable that this atlas belongs to a different species from the others.

The articular facets of the first and second atlases fit the skull to be described on page 291 better than they do the complete skull of *Pelorovis oldowayensis* on account of the former's smaller occipital condyles. The first atlas fits Pel 5 and Pel 21, but does not fit Pel 2, Pel 4 or Pel 24 any better than the complete skull. If the first three atlases are conspecific with the skull remains of *P. oldowayensis*, the problem exists of why the largest one fits only two out of the six available occipital condyles, and not even these two very well.

Axis

The most complete axis (Text-fig. 7) belongs to the same set of cervical vertebrae as the first atlas described above, and has preserved its transverse processes. A larger fossil axis has lost its transverse processes and most of its neural spine. The base of the neural spine is longer and the postzygapophyses more slanted in posterior view than in the first axis. This second axis is too large to articulate with any of the atlases but seems to belong with a second row of very large cervical vertebrae. A ventral fragment of an axis vertebra is numbered 1957 BK II 889, and by the condition of the rear of its centrum is from a young animal.

The position so far is that we have one atlas and one axis from the same complete set of cervicals, possibly belonging to a skull to be described later, and an axis from a larger set of cervicals complete except for the atlas and fifth cervical. There are three other atlases, one of which may come from another species, and an axis fragment, possibly juvenile.

Cervical vertebrae

The third cervical vertebra from the complete set is short. It has a tall neural spine and a deep posterior indentation in the neural arch—this is correlated with the shortness of the bone which brings the neural spines of adjacent vertebrae close together. The third cervical from the larger and less complete set is a longer bone and has a proportionately less deep indent posteriorly.

Measurements of the lengths of the two cervical rows were taken while they were supported in approximately their natural positions in a sandbath. The length of the complete set was 46·1 cm. from the mid-ventral point of the front of the atlas to the mid-ventral point of the back of the centrum of the 7th cervical. The length of the less complete row from the mid-ventral point of the articular rim behind the odontoid facet of the axis to the 7th cervical, allowing for the missing 5th, is 44·6 cm. So far as could be seen from mounted specimens in the British Museum (Natural History), these lengths are about the same as in Bovini.

Two other cervicals from BK II probably belong to *Pelorovis*, so too an unnumbered 7th cervical from HWK II.

Thoracic vertebrae

A well preserved but unnumbered series of thoracic vertebrae runs from about number four to number eleven. There are also parts of eighteen other thoracic vertebrae, fifteen unnumbered and the other three a series—1953, BK II Extension, 25, 26 and 27. 25–27 and an unnumbered pair are transitional to lumbars, i.e. from the back of the thoracic series. Two fragmentary first thoracics are recognizable by their very widely spaced prezygapophyses, and one of them may articulate with the seventh of the most completely preserved set of cervicals. The prezygapophyses on the first thoracic vertebra are concave. On this vertebra the foramen behind the transverse process is not closed posteriorly, but in two other anterior thoracics it is. In the most complete and best preserved set of thoracic vertebrae this foramen becomes progressively larger in the more posterior parts of the row, as is the general rule in Bovidae. There are fairly deep median indentations between the prezygapophyses. The postzygapophyses are nearer to the bases of the neural spines than in smaller Bovidae which is a difference which is better seen in anterior members of the series. The neural spines of the most complete set are tall, and the length of the tallest from the mid-dorsal point of the anterior end of the centrum to the top of the spine is 43 cm. This seems to be about usual for Bovini. The best preserved set of thoracics is not certainly from the same individual as the most complete set of cervicals.

Lumbar vertebrae

No long series of lumbars are present, but there are remains of six, all without numbers. The foramina at the side of the neural arches are small, and towards the end of the lumbar series their posterior edges are no longer closed.

Sacrum and tail

There is a fragment of a sacrum which is unnumbered, and twelve caudal vertebrae numbered 1952, BK II, 255 to 266.

III THE SYSTEMATIC POSITION OF *PELOROVIS*

It has already been noted that *Pelorovis* does not belong to the Caprinae. A far better choice for relationship is the Boselaphine-Bovine stock, but there are also a number of resemblances to *Oryx* Blainville in the tribe Hippotragini. These include the low wide skull, the horn insertions being in the same plane as the face, the absence of projecting orbital rims, the long nasals, the anterior position of the tooth rows and the characters of the teeth. The dorsal view of the *Pelorovis* skull (Pl. 1, fig. 2 ; Text-fig. 3) reminds me of *Oryx*, and the occlusal views of the molar teeth (Text-fig. 11) are similar. I shall conclude that such resemblances exist because *Oryx* has some similarities to the Bovini as a whole and not because *Pelorovis* belongs to the Hippotragini. None the less it seems desirable to include the Hippotragini with the Bovini in a detailed character comparison with *Pelorovis*. There are two living Hippotragine genera other than *Oryx*—*Hippotragus* Sundevall and *Addax* Rafinesque; the latter is similar to *Oryx* in most skull characters and need not be considered separately.

In this part of the paper bones of the living species of *Oryx* and *Hippotragus* and the Bovine genera *Bubalus* H. Smith, *Bos* Linnaeus, and *Syncerus* Hodgson will be compared to see which of them most resembles *Pelorovis*. The genus *Bos* is taken to include *Bibos* Hodgson (with the Asian species *Bos javanicus* D'Alton and *B. gaurus* H. Smith), *Bison* H. Smith, and *Poëphagus* Gray, as well as oxen in the narrow sense. The word *Bubalus* will refer only to *Bubalus bubalis* (Linnaeus) ; the small anoa, *B. depressicornis* (H. Smith), will be referred to by its full Latin name or as the anoa. The word *Syncerus* will refer only to *Syncerus caffer caffer* (Sparrman) and not to the West African bush buffalo, *S. c. nanus* (Boddaert), which will be specified separately. The English word " buffalo " will also refer only to *S. c. caffer*. Measurements, and the ratios derived from them, will be used where they are helpful ;

the methods of taking measurements have already been given. Skull measurements were taken on adult male animals, or on animals of unknown sex which could not be reliably distinguished from males, in the collections of the British Museum (Natural History). Measurements on *Syncerus* were confined to animals from East and Central Africa, these being larger than West African bush buffaloes; measurements on Hippotragini were separated according to species.

Fossil genera are considered wherever they are a source of relevant information. Among Hippotragini, fossils of *Hippotragus* are known from the Tatrot and Pinjor (Villafranchian) of India, and from South Africa (Cooke 1947). A number of early species, probably ancestral to later *Oryx* and *Hippotragus*, are known from Pikermi and other Lower Pliocene sites of Europe and Asia. Also of Lower Pliocene age are the Chinese genera *Prosinotragus* and *Sinotragus* (Bohlin 1935), which represent a group not related to later African species. *Aeotragus garussi* is a name given by Dietrich (1950) to fossil Hippotragine teeth from the Laetolil area of East Africa.

Among Bovine fossils are the extinct large and long-horned buffaloes of the African Upper Pleistocene, recognized by Bate (1951) to be closer to *Syncerus* than to *Bubalus*, and given by her the generic name *Homoioceras*.[1] I have seen the cast of the Sudanese *H. singae* Bate in London; a cranium with partial horn cores, another horn core and a few limb bones of the North African *H. antiquus* (Duvernoy) in Paris; and the skeleton of *H. nilssoni* (Lönnberg) from Malewa near Naivasha, Kenya and now in Stockholm. I agree with Miss Bate about the resemblance of these animals to *Syncerus*, indeed there is at least a possibility that they might include the ancestors of the living species which can be regarded as specialized in its skull proportions and small horn cores.

Simatherium kohllarseni is a name given by Dietrich (1942) to a buffalo-sized Bovine from the beds in the Laetolil area, which are thought to be slightly older than Bed I at Olduvai.

Leptobos Rütimeyer is the Villafranchian ox of Europe and India, differing from the closely related *Bos* by having less posteriorly inserted horn cores, and by other characters associated with this. The earliest examples of *Bos* are contemporary with *Leptobos*; they are the large and long-horned *B. acutifrons* Lydekker from the Indian Pinjor, and *B. sivalensis* (Lydekker) and *B. palaeosinensis* (Teilhard de Chardin & Piveteau) which are two bison from the Pinjor and from Nihowan in China. Later in the Pleistocene comes the great extinct Palaearctic ox *Bos primigenius* Bojanus, with its Indian subspecies *B. primigenius namadicus* (Falconer) which had somewhat longer horns with a posterior keel towards their base.

Hemibos Falconer is an extinct Villafranchian genus from India and Palestine (Pilgrim 1941) related to *Bubalus*; it differs from *Leptobos* by having keeled horn cores, longitudinally convex frontals between the horn bases, and a braincase more bent down on the facial axis.

Proamphibos Pilgrim from the Dhok Pathan and Tatrot (Pliocene and earliest Pleistocene) of India is smaller than *Hemibos*, and could be its ancestor. A contemporary genus from Europe is *Parabos* Arambourg and Piveteau. A cranium of *P. cordieri* (Christol) from Montpellier and a skull and cranium of *P. boodon* (Gervais) from Perpignan are available in Paris, together with more fragmentary pieces. The teeth of these animals are slightly less advanced than in *Proamphibos*. It is not necessary to continue the list of fossils ; all that need be said is that there is little doubt that later Pliocene Europe and India were inhabited by a variety of Boselaphine or Bovine species, not all of which need have phyletic connections with later Bovini. Teeth in the palaeontological collections at Uppsala show that similar animals inhabited later Pliocene China. It is an as yet unanswered question whether the ancestry of *Syncerus*, like that of *Bubalus* and *Bos*, lies among these animals, or whether its progenitors were by then already living in Africa, having separated from the Eurasian stock at an earlier date.

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[1] The name *Homoioceras* actually dates from 1949 (see Bate 1951).

1. It may be noted at the outset that the large size of *Pelorovis* is a good reason for thinking it to be Bovine ; Hippotragini are medium to large Bovidae, and although there are small Bovini such as the anoa, the progress of evolution through Boselaphini to Bovini has usually been accompanied by increasing size. According to measurements of skull length and length of upper molar row (Text-fig. 9) *Pelorovis* is large among Bovini ; in orbital width as a measure of size it is easily exceeded by *Bos primigenius* ; while its femur length is less than in *Homoioceras nilssoni*, *Bubalus*, or *Bos primigenius*. The largeness of Bovini hinders comparison with other Bovid

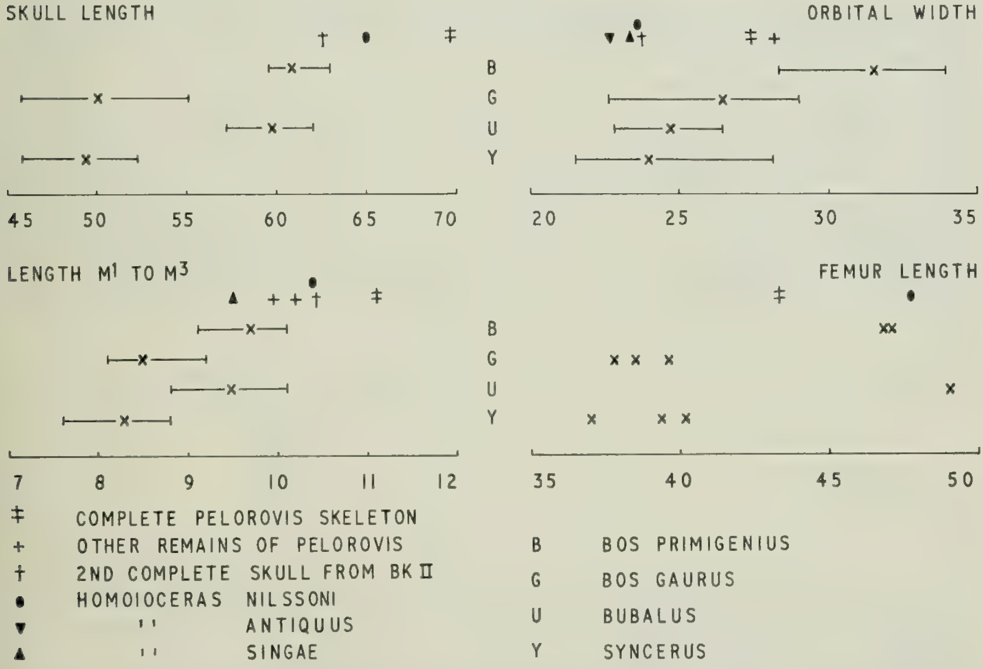


FIG. 9. Four diagrams to show the size of *Pelorovis oldowayensis* in relation to some Bovini. Individual readings are shown for African fossils and for the femur lengths of all animals ; in other cases the mean value and observed range are shown. Measurements in cms.

tribes because I am so often unsure about the extent of allometric influence on the characters.

2. A comparison of general skull proportions shows that *Syncerus* has a wide skull with a shortened facial region ; that *Bubalus* has a narrower skull with a longer face ; and that *Bos* is very wide across the frontals, with oxen having a long face and bison a shortened face. In *Hippotragus* the skull is high and narrow and although *Oryx* does have a broader and lower skull than *Hippotragus*, this is not carried so far as in the larger Bovine genera, for which allometry must be largely the deciding factor. *Pelorovis* is closest to *Bubalus* in these proportions, but if the supposed allometry is taken into account it could equally be considered to be like *Oryx*.

The two ratios of length from the premaxilla tip to the front of the orbit as a percentage of skull length and orbital width as a percentage of skull length give quantitative indications of skull shape. Readings for the first ratio in Bovini were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	18	7	9	4
Mean value . .	53·3	59·9	56·5	63·4
Range . . .	49·7–56·4	57·4–61·9	54·3–58·2	62·4–63·7

The face of *Syncerus* is shorter than in the two *Bos* species or *Bubalus*, although this effect might be less pronounced in females and the smaller West African bush buffaloes which have not such large basal bosses to their horn cores. The reading for *Homoioceras nilssoni* was 52·8—close to that for *Syncerus*, and for the complete skull of *Pelorovis* 61·6—close to *Bos primigenius*. Hippotragini have values from 59·6 (mean of three *Addax*) to 63·8 (mean of five *Oryx beisa*), i.e. their faces are as long as in *Bubalus*, *Bos primigenius* and *Pelorovis*. However in *Hippotragus niger* the component of length of face in this ratio has been increased by the bending of the braincase on the facial axis. *Hippotragus equinus* has a slightly longer braincase ; its appearance of having a very long braincase is caused partly by the height and narrowness of its skull and partly by the uprightness of its horn insertions.

Readings for the ratio orbital width as a percentage of skull length were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	18	7	9	4
Mean value . .	48·7	41·2	52·3	55·1
Range . . .	44·8–53·7	39·0–44·0	48·0–56·0	47·5–64·5

Bos is very wide at the orbits, due to expansion of the frontals, while *Bubalus* is rather narrow, and *Syncerus* is intermediate. The value for the complete skull of *Pelorovis* is 39·8, which is narrower than the mean for *Bubalus*, but in male animals with bigger horns the orbital width would probably have been greater. In *Homoioceras nilssoni* the value was *c.* 36·3, the orbits of this specimen being probably closer together than in either the *H. antiquus* or *H. singae* specimens. Hippotragini have values from 38·1 (mean of six *Hippotragus niger*) to 44·2 (mean of three *Addax*). Length of face also affects the dimensions of the nasals and the position of the tooth row, both of which will be considered later.

3. Among living forms horn cores are long in Hippotragini, long in *Bubalus*, intermediate or short in most *Bos*, and short in *Syncerus*. The African *Homoioceras* had very long horns, and so too did the Indian *Bos acutifrons* which is older than *Pelorovis*. This character is obviously not useful in determining the affinity of *Pelorovis*.

4. The horn cores are straighter in *Oryx*, except in *O. algazel*, than in the other genera considered here, and *Oryx* is also unlike *Pelorovis*. The torsion of the horn cores of *Pelorovis*, in so far as it exists, is clockwise from the base upwards in the right horn core, which is the same as in *Leptobos*, *Bos* and *Syncerus*. The difference between weakly clockwise and weakly anticlockwise torsion is slight, so even were *Pelorovis* different from the Bovines, it would count for little. However the actual course of the curvature as opposed to the torsion of the horns of *Pelorovis*, as seen in Pl. 1, fig. 2, consists first of a backwards swing, then of one to the front, whereas in *Homoioceras* the swing is at first forwards then backwards; i.e. the horns of *Homoioceras* are on a different arc of a clockwise circle. The curvature of *Pelorovis* horns is like that of long-horned species of *Bos*.

5. At the present time dorso-ventral compression of the horn cores is more pronounced in *Syncerus* than in *Bos*, with *Bubalus* being intermediate. Measure-

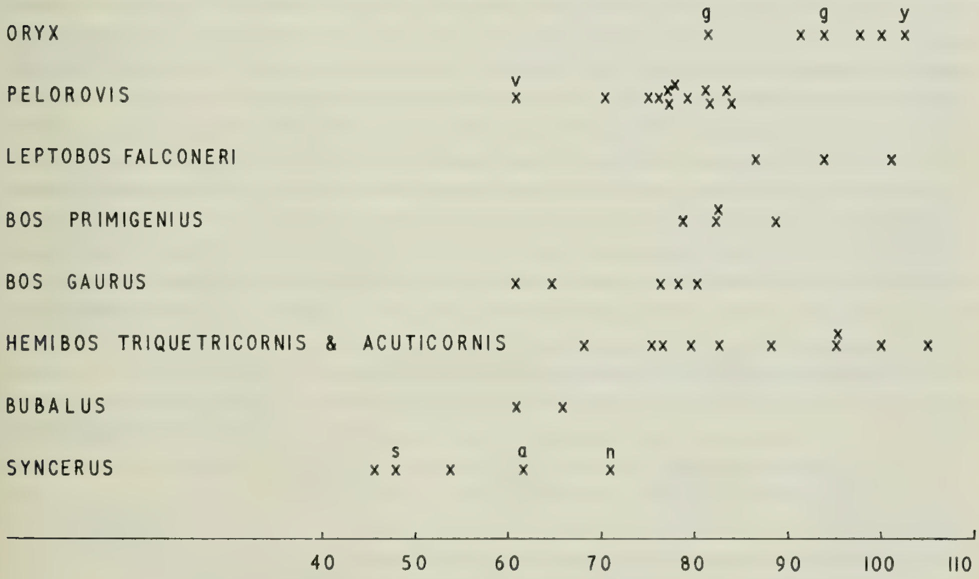


FIG. 10. Histogram of dorso-ventral diameter of horn cores as a percentage of transverse diameter. *g* = *Oryx gazella*, *y* = *O. algazel*; the remaining three *Oryx* belong to *O. beisa*. *v* = the second complete skull from Olduvai BK II, *s* = *Homoioceras singae*, *a* = *H. antiquus*, *n* = *H. nilssoni*. One specimen of *Hemibos* had a ratio of 126.8.

ments are difficult to take, but it does seem (Text-fig. 10) that the horn cores of *Leptobos* are less compressed than in *Bos*, *Hemibos* than in *Bubalus*, and *Homoioceras* possibly less than in *Syncerus*. Therefore it is not possible to say that *Pelorovis*, with its slight compression, resembles one Bovine group rather than the others. *Oryx* has almost rounded horn cores (although there are probably valid differences among the species for this), but *Hippotragus* has transverse compression.

6. Keels on the horn cores are absent in *Pelorovis*, in living and most fossil Hippotragini, in *Bos* except for the Indian *B. acutifrons* and *B. primigenius namadicus*, and in *Leptobos*. They are present in *Bubalus*, *Hemibos* and *Proamphibos*, and in West African bush buffaloes. Those in larger *Syncerus* and in *Homoioceras antiquus* appear to be a result of the compression of the horn cores, and they are less marked in the less compressed horn cores of *H. nilssoni*. All that emerges with certainty from this character is that *Pelorovis* is unlike the *Bubalus* group.

7. Among Bovini the earlier species have more nearly uprightly inserted horn cores in lateral view, but later in evolution their basal parts come to be more nearly in the plane of the face. The horn cores of *Hippotragus* are more uprightly inserted than in any other genus considered here; however, those of *Oryx* are in the plane of the face as in later Bovini, and this state was acquired earlier in the *Oryx* stock than in Bovini as witnessed by the Lower Pliocene *Palaeoryx*. This character is therefore of little use in helping to decide the tribal affinity of *Pelorovis*, since the Bovini lie between the two Hippotragine extremes.

8. The horn cores of Bovini arise behind the orbits. In larger *Syncerus* their front edges are more anterior than in comparably sized *Bubalus*. Some *Bos* species have very posteriorly-sited horn cores, so much so that they may overhang the occipital surface of the skull, and for this character *Bos* most resembles *Pelorovis*. Horn cores are inserted behind the orbits in *Oryx* but not in *Hippotragus*, the difference here being linked with the angle of insertion of the horns.

9. In larger *Syncerus* the great basal bosses bring the horn cores closer together than in the larger *Bubalus*, while *Bos* has horn cores set far apart on its wide frontals. Hippotragini have closer insertions than Bovini, and within the Hippotragini *Hippotragus* has closer insertions than *Oryx*. The question of how widely apart horn cores are inserted is not always easy to decide since increasing size of horn cores in evolution may bring their bases close together, and also because backward migration of the horn cores must sometimes allow them to become more widely inserted; this last factor is perhaps responsible for their greater separation in *Oryx* than in *Hippotragus*. In *Pelorovis* there is no doubt that the horn cores are set close together. This may be appreciated by comparing the Indian *Bos acutifrons* (Lydekker 1878, pls. 12, 13), which appears to have horn cores of about the same size and with a similar curvature to *Pelorovis*, with Pl. 1, fig. 2 and Pl. 2, fig. 3 in this paper. The contrast between *Pelorovis* and any species of *Bos* for this character suggests that both genera have evolved their posterior horn insertions independently.

10. Both sexes have horns in even the earliest known Hippotragini; in the Bovini all Recent species except the anoa have horned females, but the fossil genera *Hemibos*, *Proamphibos*, *Leptobos* and the skull which Pilgrim (1913, 1939) called *Proleptobos* all have, or are, hornless females. The fact that I interpret *Pelorovis*

to have horned females is of no consequence, since it occurs late enough to have evolved from ancestors with or without horned females.

11. In Bovini the parieto-frontals' suture has a forwardly pointed indentation between the horn bases, although it is usually invisible in adults. In living Hippotragini it is transversely directed without anterior indentation between the horns, but early Chinese and European Hippotragini had such an indentation like Bovini. One might expect some correlation between shape of the suture and antero-posterior position of the horn cores; however in such earlier Bovine genera as *Leptobos*, *Hemibos* and *Proamphibos* the suture does lie behind the level of the horn cores, but is none the less anteriorly indented in the centre of its course across the top of the skull. This character is not useful in relation to *Pelorovis*, since its horn cores are so posterior that the suture would be bound to be indented, even were it visible in a single specimen. The suture is straight in living *Boselaphus* Blainville, but this animal is probably remote from Bovine lineages.

12. Temporal fossae are present behind the orbits in *Pelorovis* and in Bovini, but their presence is at least partly correlated with the massiveness of the horn bases, and thus with the size of the animal, and also with the generally posterior position of the horn insertions in Bovini. They are absent in Hippotragini.

The character of temporal crests behind the horns ought to be mentioned here. Their presence or absence is said by Pilgrim (1939 : 148–149) to be correlated with the degree of bending down of the facial on the basicranial axes. The axes are at an angle to one another in Hippotragini, and temporal crests are not found. Originally the axes were little bent on one another in Bovini and their ancestors, hence temporal crests are found in *Proamphibos* and *Leptobos*. However *Hemibos* has developed a greater angle between the axes (the longitudinal convexity of the frontals between the horn bases is probably linked with this), and *Bos* has moved its horn cores to a more posterior position, thereby doing away with the need or possibility of temporal crests. The horns are so large in *Bubalus* and have such large bosses in *Syncerus* that there is no room for temporal crests, but it is not easy to say whether the facial axis is more bent on the basicranial axis than in *Leptobos* and *Proamphibos*, and whether the convexity of the frontals in the small bush buffaloes and small examples of *Bubalus bubalis* are comparable with that in *Hemibos*. It is apparent that *Pelorovis*, having horn insertions as far back as in *Bos*, could not have temporal crests.

13. The supraorbital pits are relatively closer together in Hippotragini than in Bovini. Readings for the distance between the supraorbital pits as a percentage of orbital width in Bovini were:

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	21	8	10	4
Mean value . .	51·1	58·1	56·6	57·6
Range . . .	42·2–59·5	55·1–61·9	43·2–72·2	55·2–62·2

The closeness of the supraorbital pits in *Syncerus* could be interpreted by supposing that the growth in size of their basal horn bosses, particularly in males, must have caused an increase in orbital width. *Bubalus* and *Bos* have supraorbital pits which are wider apart than in *Syncerus*. The values for *Homoioceras singae, H. antiquus* and *H. nilssoni* were 50·4, *c.* 49·3 and *c.* 65·2, the last value probably reflecting that specimen's narrowness across its orbits. The value for the complete *Pelorovis* skull was 42·3 and for Pel 3 53·2. In Hippotragini the values for this ratio extend from 42·3 (a single *Oryx leucoryx*) to 47·3 (the mean of five *O. beisa*), thus supraorbital pits are closer together than in Bovini.

A point to be remembered is that the antero-posterior position of the supraorbital pits may influence their transverse separation from one another. They are more anteriorly sited in *Syncerus* (and some bison) than in *Bubalus* or *Bos* (other than bison), so that they have less space in which to be wide apart. This factor would, however, have little effect on the difference between *Bos* (other than bison) and *Syncerus* compared with the effects of the wider frontals of *Bos*. This factor does not seem to apply to *Pelorovis*, which has supraorbital pits set more posteriorly than in *Syncerus* or *Bubalus*, but none the less close together.

14. The orbital rims are strongly projecting in *Bos* (especially in bison species), less so in *Bubalus*, while in *Syncerus* such tubularity occurs only in few individuals. The orbits usually protrude little in Hippotragini except in *Hippotragus equinus*. The small bush buffaloes of West Africa have horn cores which are close to the orbits, and, being directed diagonally backwards at their bases, prohibit the development of tubularity in the orbits, but this explanation does not apply to the absence of tubularity in most larger *Syncerus*. The orbits of *Pelorovis* do not project very strongly, thus making it most like Hippotragini or *Syncerus*.

15. The nasals of *Oryx* are flatter across their upper surface than in the other genera considered here.

16. The nasals are wide in *Bos*, slightly less so in *Syncerus*, and narrow in *Bubalus*. This character can be assessed quantitatively by taking nasals' breadth as a percentage of nasals' length, and nasals' length as a percentage of skull length. The readings for the first ratio in the Bovini were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	14	5	9	2
Mean value . .	33·2	26·2	36·6	35·5
Range . . .	25·7–40·1	22·0–30·6	31·3–39·8	35·2 & c. 35·8

Width of nasals is a variable dimension.

Readings for nasals' length as a percentage of skull length were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	16	5	8	2
Mean value . .	39·8	42·4	43·8	43·0
Range . . .	34·1–43·8	40·3–45·8	39·9–48·0	42·4 & c. 43·6

Homoioceras singae had a value of *c.* 37·6 for the first ratio, but *H. nilssoni* could not be measured.

Despite its very long and narrow nasals according to the first ratio, *Bubalus* has nasals no longer relative to skull length than in the *Bos* species. The complete skull of *Pelorovis* has a value of *c.* 21·4 for the first ratio and *c.* 46·2 for the second; these could be taken as showing great length of the nasals (presumably linked with the long face) rather than narrowness, especially as the nasals are wider in their front half than in their back half (Text-fig. 3). Hippotragine readings for the first ratio ranged from 18·75 (mean of six *Hippotragus niger*) through 21·3 (mean of nine *H. equinus*) to 30·9 (mean of five *Oryx beisa*), and for the second from 36·2 (one *O. leucoryx*) to 42·5 (mean of three *O. gazella*). Thus *Pelorovis* is nearest to *Bubalus, Oryx* and possibly *Hippotragus equinus* for the first ratio, while for the second it is near the extreme for either tribe.

17. Lateral flanges at the anterior end of the nasals are pronounced in *Bubalus, Bos javanicus* and some *B. gaurus*, and practically absent in other *Bos* species, *Syncerus* and *Homoioceras*. They are present in *Hemibos* if the skull 23109 at the British Museum (Natural History) is indeed of *Hemibos*, although Pilgrim (1937, fig. 47*c*) has drawn the genus without them. They are absent in Hippotragini. In the complete skull of *Pelorovis* they are clearly absent.

18. A transverse expansion at the back of the nasals is present in *Bubalus* and *Hemibos* and in some *Syncerus*, and absent in *Bos*, Hippotragini and *Pelorovis*.

19. The posterior end of the nasals is in front of or barely level with the front of the orbits in Hippotragini, but lies slightly more posteriorly in Bovini, except that some individuals of *Bos* may overlap *Hippotragus* individuals. This character is unlikely to be caused by allometry because in the anoa the back of the nasals is level with the front half of the orbits and in the large Caprine *Ovibos* Blainville they start in front of the orbits. The position of the suture is not certain in *Pelorovis*, but it appears to be level with the front half of the orbits.

20. The nasals of *Syncerus* are often more nearly parallel to the tooth row in profile than in *Bubalus*; *Bos* appears to be nearer to *Bubalus* than to *Syncerus*, and the Hippotragini are like *Bubalus*. This is not a useful character in *Pelorovis*. The reconstruction of its skull in lateral view (Text-fig. 2) does show the nasals in a position similar to *Syncerus*, and the drawing was made before I was aware of the *Syncerus* character, but one would need the preservation of an undistorted skull before accepting this character.

21. The absence of an ethmoidal fissure in the complete skull of *Pelorovis* makes it unlike *Oryx* and also unlike *Hippotragus* in which the existing fissure has become blocked by underlying bone. It is less unlike early Hippotragini in which the fissure is often small or difficult to see. Among Bovini it is more like *Syncerus* and *Bubalus* than *Leptobos* or *Bos* in which the fissure can often be seen at least until the early part of adult life.

22. The preorbital fossa is absent or only faintly indicated in Bovini, and is shallow in early Hippotragini (but deep in *Sinotragus*) and absent in later ones; thus its absence in *Pelorovis* gives no indication of possible tribal relationship.

23. The deep zygomatic bar of *Pelorovis* is a character seen in the Alcelaphines *Damaliscus* and *Alcelaphus*, and also in the skull of *Homoioceras nilssoni*. I think that its appearance is connected with the mechanics of supporting the horn cores.

24. The position of the infraorbital foramen is a distinguishing character between Hippotragini and Bovini. It is found in *Oryx* relatively high above the tooth row

and relatively posteriorly sited, whereas in *Bubalus* and *Syncerus* it is lower and further forwards, perhaps in front of P^2. *Bos* and *Hippotragus* may not always be distinguishable, but their foramina are often near to the positions occupied in their respective tribes. The foramen of *Pelorovis* is undoubtedly in a Bovine position.

25. The size of the palatal fissures between maxillae and premaxillae varies among the genera considered here. They are large, chiefly noticeable in their great length, in *Hippotragus*, but much smaller in *Oryx*. In Bovini they are smaller in *Bubalus* and *Syncerus* than in *Bos* but not as small as in *Oryx*. In *Pelorovis* only the front parts of the fissures are present, but I would judge them to lie between *Oryx* and *Syncerus* in size.

26. In the Hippotragini the premaxillae make or just avoid making a short contact with the nasals ; this character is less constant within Bovine genera, but *Syncerus* appears to be nearest to the Hippotragine condition. In *Bos* the premaxilla often falls well short of a contact with the nasals, but in *Bubalus* it invariably has a long contact. The premaxilla of *Pelorovis* is closest to the condition of *Syncerus* and Hippotragini.

27. The tooth row is set more anteriorly in some *Bos*, e.g. *B. grunniens* (the yak) and *B. primigenius*, than in other Bovini, and in *Oryx* and *Hippotragus niger* than in *H. equinus*. This character can be linked with the more posteriorly sited orbits of the *Bos* species, *Oryx*, and *Hippotragus niger*, and can be quantitatively expressed by the length from the premaxilla tip to M^3 expressed as a percentage of the length from the premaxilla to the nearest point of the orbit :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	19	8	10	3
Mean value . .	108·8	101·0	108·8	89·1
Range . . .	102·8–114·8	97·3–103·5	106·3–111·5	88·1–90·1

Readings for Hippotragini pass from 91·1 (mean of five *Oryx beisa*) to 98·8 (mean of ten *Hippotragus equinus*). The reading for the complete skull of *Pelorovis* is 82·3, which is most nearly approached by *Bos primigenius* in the above table. In *Homoioceras nilssoni* the reading is 97·4 ; this is most interesting because this animal has as short a face as in *Syncerus*, as was seen on page 268 above. It is thus less remote from *Pelorovis* for this proportion than are the *Syncerus* in this sample.

This is perhaps a good place to sum up the differences in skull shape revealed by the last ratio and those under characters 2 and 13 above. *Syncerus* has a very short face as shown by the anterior position of its orbits, although this effect is likely to be exaggerated in males. In *Homoioceras nilssoni* too the face is short, but the skull is narrower across the orbits, and the tooth row is situated more anteriorly. *Bubalus* has a longer face and a less posteriorly placed tooth row, presumably correlated features. It is narrow across the orbits but less narrow than in *Homoioceras nilssoni*, and its supraorbital pits are not so anterior or so close as in *Syncerus* and the three *Homoioceras* species. *Bos* is characterized by a wide frontals region, and agrees with *Bubalus* in having supraorbital pits set widely apart and posteriorly. Some *Bos* may have long faces and tooth rows set far forwards as do *B. primigenius* and *B.*

grunniens. *Pelorovis* has a long face, is narrow across the orbits, and has a markedly anterior tooth row. It differs from *Syncerus* in all these features, and from *Homoioceras nilssoni* in its long face and to a lesser extent in the position of its tooth row. It differs from *Bubalus* in its more anterior tooth row, and from *Bos* in its narrow width across the orbits and very slightly in the position of its tooth row. The Hippotragini have longer faces than some Bovini, are narrow across the orbits, and their supraorbital pits are more anterior and closer together.

28. The level of the median indentation at the back of the palate is a good distinguishing character between Hippotragini and Bovini. In Hippotragini it is level with the lateral ones or slightly anterior or posterior. *Bubalus* is the Bovine most remote from the Hippotragini, by having a long backwards extension of the median part of the palate taking the indentation well posterior to the lateral ones. This also occurred in *Hemibos* and *Proamphibos*. Many individuals of *Syncerus* are less remote from the Hippotragine condition, while *Bos* lies between *Syncerus* or *Bubalus*. In *Pelorovis* the median indentation is anterior to the lateral ones, more so than in many Hippotragini, and if *Pelorovis* is a Bovine this character is no longer distinctive for the two tribes.

29. The vomer is fused with the back of the palate in *Bubalus bubalis*, *B. depressicornis* and *Hemibos*, but not in *Pelorovis* or any other genus considered here. Pilgrim (1939 : 274) states that fusion probably occurred in *Proamphibos*.

30. The occipital surface of the skull is low and wide in *Bos gaurus* and *Syncerus*, but higher in *Bubalus* and *Bos primigenius* ; it is also lower in *Oryx* than in *Hippotragus* especially *H. niger*. Readings for the height of the occiput as a percentage of its width were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	18	5	9	4
Mean value . .	31·9	37·5	32·0	36·3
Range . . .	28·8–36·5	34·4–39·8	29·4–35·3	32·7–40·1

The reading for *Homoioceras singae* was 31·7, for *H. antiquus* 32·3, and for *H. nilssoni* 31·9, which agree very well with *Syncerus*. The readings for Hippotragini range from 35·6 (one *Oryx leucoryx*) to 52·0 (mean of six *Hippotragus niger*), readings which are rather higher than in Bovini. Three values for *Pelorovis* are 40·7, 36·9 and 35·5, making it unlike *Syncerus* and *Homoioceras*, but more like *Bubalus*, *Bos primigenius* or *Oryx*. The difference between the size of horns in male and female cattle was found by Howard *in* Mourant & Zeuner (1963 : 96) to affect this ratio, male animals having a lower occiput.

31. The mastoid exposure of the periotic is entirely on the occipital surface in Bovini, including the anoa, and in *Oryx*, but in *Hippotragus* it is visible in lateral view as well. In *Pelorovis* it is on the occipital surface.

32. The top edge of the foramen magnum is more posterior relative to the occipital condyles in *Oryx* than in *Hippotragus* in which the paraoccipital processes are markedly anterior relative to the condyles. *Pelorovis*, Bovine genera and Lower Pliocene Hippotragini are intermediate for this character.

33. The distance across the anterior tuberosities of the basioccipital is a variable dimension ; it is narrow in *Syncerus*—perhaps because the main mass of the horn cores is concentrated in their basal bosses, wider in *Bos* and *Bubalus*, and wider still in Hippotragini. Often in *Syncerus* there is a transverse narrowing immediately in front of the posterior tuberosity which gives the bone a more quadrangular appearance than would be expected from its measurements. Readings for the width across the anterior tuberosities as a percentage of the width across the posterior ones were :

	Syncerus	*Bubalus*	*Bos gaurus*	*Bos primigenius*
Number measured .	19	7	9	3
Mean value . .	45·9	53·7	55·2	49·3
Range . . .	36·6–55·9	47·7–59·4	46·2–65·0	46·2–53·4

The reading for *Homoioceras singae* was 50·0, for *H. antiquus* 45·0, and for *H. nilssoni* 54·7 ; probably these animals had wider tuberosities than living *Syncerus*. The three available readings for *Pelorovis* were 53·8, 57·6 and 58·4—all rather wide compared with the readings in the above table. But there can be no doubt that for this character *Pelorovis* shows Bovine affinities ; the living Hippotragini range from 73·3 (mean of three *Oryx gazella*) to 107·7 (one *O. leucoryx*). Early fossil Hippotragini are scarcely less different, as the four following readings on fossils from Pikermi in the British Museum (Natural History) show :

M.10832,	*Palaeoryx woodwardi*	80·0
M.11415, M.10839,	*Protoryx carolinae*	71·8 and 72·5
M.10833,	*Microtragus parvidens*	83·7

Hippotragus has anterior tuberosities which have grown large and have expanded to some extent laterally. In the course of expansion a longitudinal ridge has tended to build up behind each tuberosity, leaving a deep groove running along the centre of the bone. In *Oryx* the anterior tuberosities are smaller and more localized, without the development of longitudinal ridges. In Bovini the anterior tuberosities are not so localized as in *Oryx*, nor are they so expanded as in *Hippotragus*. *Pelorovis* could be said to be like *Oryx* or Bovini in this.

34. The foramina ovales are large in living Hippotragini, especially in *Oryx*, but even in *Hippotragus* they are larger than is usual in Bovini, although there is a good deal of overlap. They are smaller in some lower Pliocene Hippotragini. The foramina are sufficiently small in *Pelorovis* for it to resemble the Bovini (or early Hippotragini) for this character.

35. An indentation in the squamosal shelf immediately in front of the mastoid occurs in *Oryx*, Bovini and *Pelorovis*, and can be seen in ventral view (Pl. 2).

36. The size of the auditory bulla is probably not a good distinguishing character unless one is dealing with undoubtedly closely related forms, so it is here of doubtful validity. It is less inflated in *Bos* and *Bubalus* than in *Syncerus* and Hippotragini. In *Pelorovis* it is within the range of *Syncerus* and Hippotragini.

37. The upper molar teeth are wide in *Hippotragus* and Bovini, but not in *Oryx*. Within any one genus the width of the molars is a variable dimension, but during their evolution the Bovini have undoubtedly widened their molars. The widening is partly connected with increasing size, but large Bovidae such as *Taurotragus* Wagner and *Ovibos* do not have noticeably wider upper molars than their smaller relatives. *Pelorovis* has molars as wide as in *Hippotragus* and Bovini. This character, and others of the teeth, are illustrated in Text-fig. 11.

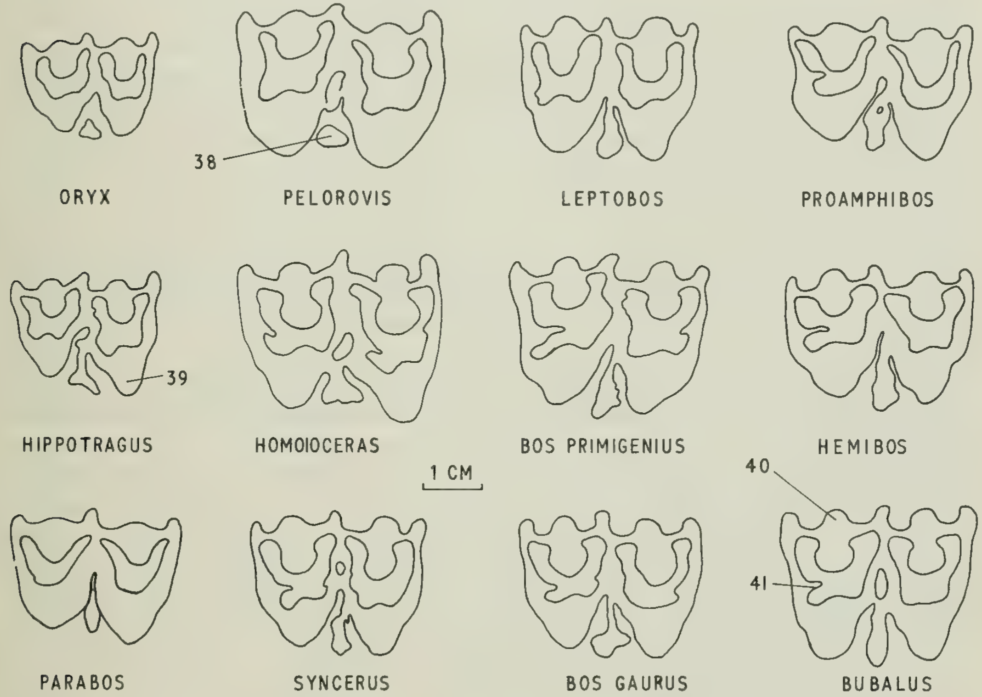


Fig. 11. Occlusal views of right M^2 in some Bovid genera. The anterior side is towards the right side of the page. The numbers are those by which characters are referred to in the text.

38. Basal pillars on the molar teeth are small in *Oryx*, but large and complicated in *Hippotragus*; they are also large and complicated in Bovini. Within the Bovini this character is affected by allometry since *Syncerus* and smaller *Bos* have smaller basal pillars than *Homoioceras*, *Bubalus* and larger *Bos*. However those of *Pelorovis* are small despite the large size of its teeth.

39. The medial lobes of the upper molars are less narrowed in *Oryx* than in *Hippotragus*. Neither *Pelorovis* nor the Bovine genera being considered here have lobes as narrow as in *Hippotragus*.

40. Localized outbowings on the lateral walls of the molars are well marked in *Bubalus* and some *Bos*, but less so in *Syncerus* and smaller *Bos*; this is again likely

to be influenced by allometry. They are better marked in *Hippotragus* than in *Oryx*, as can be seen in Text-fig. 11. They are hardly present in *Pelorovis*.

41. *Syncerus* and some *Bos* have a slightly less complicated course of the enamel borders of the central cavities of the upper molars than in *Homoioceras*, *Bubalus* or larger *Bos*, which is probably allometric although *Oryx* certainly shows less complication than the equally sized *Hippotragus*. *Pelorovis* agrees with *Oryx*.

42. The front edge of the coronoid process of the lower jaw is strongly curved to fit the temporal fossa in Bovini other than *Homoioceras nilssoni* and some *Bos* such as *B. grunniens* and *B. primigenius*. In *Pelorovis* (Pl. 6) and *Oryx* there is little curvature as in the *Homoioceras* and two *Bos* species, while in *Hippotragus* the curvature is not much stronger. It may be noted that the lack of strong curvature in *Pelorovis*, *Homoioceras nilssoni* and some *Bos* is connected with the anterior position of the tooth row, in *Hippotragus* the absence of a temporal fossa has an effect, and in *Oryx* both factors may have acted.

43. The horizontal ramus of the lower jaw is deep in the Hippotragini and in *Pelorovis* (Pl. 6).

44. The lower molars of *Oryx* have weaker goat folds than in *Hippotragus*. They are absent in the Bovini and in *Pelorovis*. Goat folds are transverse expansions of the most anterior part of the lower molars separate from the main mass of the anterior lobes.

45. The central cavity of the anterior part of P_4 is open medially to the outside of the tooth in Hippotragini, *Bubalus* and *Bos*. It is enclosed by a medial wall in *Syncerus* (except that in 62.219 at the British Museum (Natural History) it is open on the left and closed on the right). It is also open in *Homoioceras nilssoni*, but the medial wall has only just failed to close. It is closed or almost closed in all *Pelorovis* (Pl. 3, fig. 2 ; Pl. 6, fig. 3) except in the lower jaws (M.15856) from Kanjera. This character is useful for differentiating African from Eurasian Bovini.

Colbert & Hooijer (1953 : 119–20) found that *Bubalus* never has a small accessory column between the hypoconid and talonid as is seen in some *Bos gaurus*, and that it has a greater tendency to have the posterior medial valley of older P_3s and P_4s forming an isolated fossette.

46. The length of the premolar row may be quantitatively expressed as a percentage of the length of the molar row, but the results are not very useful because only small numbers of animals could be measured. In Pel 23, an old animal, the ratio for the upper dentition is 60·8. This is low compared with the Bovine range from 60·9 for one *Syncerus* to 70·6 which was the mean for two *Bos gaurus*. Eleven *Syncerus* had a mean value of 65·5, *Homoioceras nilssoni* had a reading of *c.* 63·5, four *Bubalus* a mean of 68·8, and one *Bos primigenius* a reading of 64·4. In the Hippotragini *Hippotragus equinus* has a very long premolar row with a mean value of 74·8 and a range from 70·7 to 79·4 for ten specimens, *H. niger* has a shorter row with a mean of 67·4 and a range from 65·8 to 69·2 for five specimens, and *Oryx* species have readings mostly below 60 except that the mean for five *Oryx beisa* rises to 60·9. These differences presumably indicate differences in Hippotragine feeding habits.

In lower jaws two values for *Pelorovis* at 50·9 and 58·5 have a mean less noticeably different from Bovini than was the value for the upper jaw. The mean of five

Syncerus was 58·7, of two *Bubalus* 59·0, and seven *Bos gaurus* 57·5. It is obvious from discrepancies between upper and lower dentitions that larger samples are needed to clarify the facts, but one may tentatively conclude that *Pelorovis* had rather shorter premolar rows than in living Bovini.

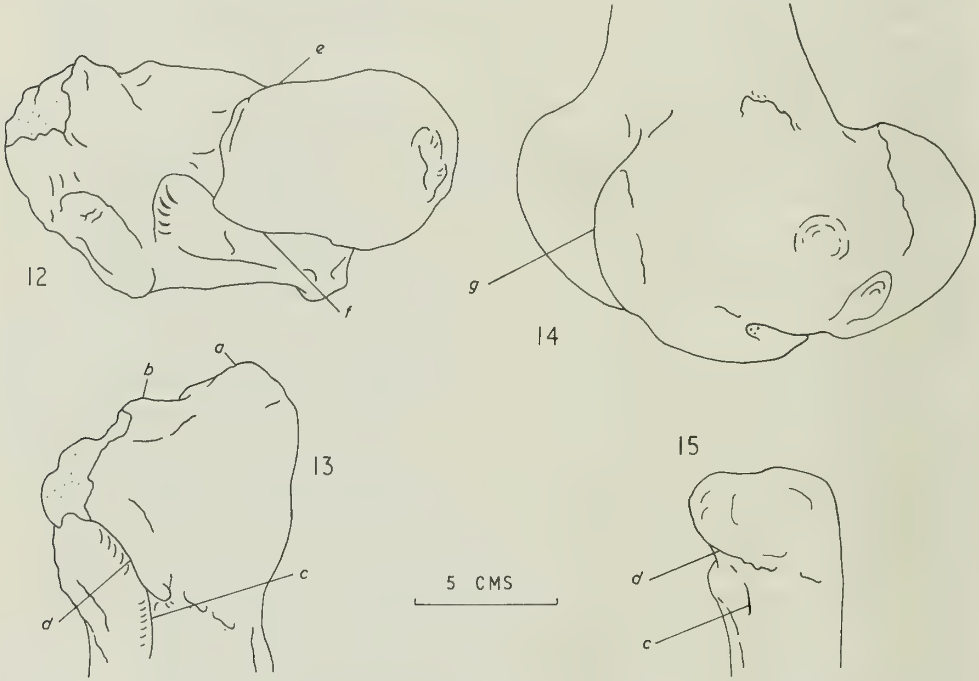
47. For the ratio of length of P^2 or P_2 in relation to the length of the total premolar row, *Pelorovis* seems to lie at about the centre of both Bovine and Hippotragine ranges. It is not possible to find trustworthy differences without more specimens to measure.

To sum up the tooth characters, while the teeth of *Oryx* are not greatly advanced other than in their hypsodonty, the course of morphological evolution has some similarities in Bovini and *Hippotragus*, i.e. increasing width of the upper molars, increasing size of the basal pillars, stronger and more localized outbowings of the lateral walls of the upper molars, and a more complicated outline of the enamel borders to the central cavities. However *Hippotragus* differs from Bovini in other details : basal pillars are often Y-shaped in section and are extremely large for the size of the teeth, lateral outbowings of the upper molars are smaller, borders of the central cavities are less complicated, and there are goat folds on its lower molars. *Pelorovis* therefore resembles *Oryx* in possessing a moderate development of hypsodonty without a very advanced pattern of the occlusal surfaces. It is also like Boselaphini and early Bovini in its occlusal pattern, differing from a form like *Parabos* only in being more hypsodont and having wider upper molars, so that if *Pelorovis* is a Bovine genus, then it is one with primitive teeth. The influence of body size on tooth characters is great, and it is possible that a *Parabos*, growing to a size equivalent to that of *Pelorovis*, would acquire wider and more hypsodont molars. It is also true that while the living Bovini have more advanced teeth than *Pelorovis*, it is the larger species which differ more. *Syncerus* has less advanced teeth than *Bubalus* in several characters mentioned above, but *Syncerus* is a smaller animal ; the upper molars of the closely related, larger *Homoioceras nilssoni* (Lönnberg 1933, pl. 1, fig. 4) are no less advanced than those of *Bubalus*. Within *Bos* too it is the larger animals which have the closest resemblance to *Bubalus*.

The comparisons of limb bones and vertebrae were based on material in the Osteology Room at the British Museum (Natural History) : five skeletons of Chillingham and Chartley cattle, three *Bos gaurus*, one *Bos grunniens*, one *Bubalus bubalis*, three *Syncerus caffer*, three *Hippotragus niger*, two *H. equinus* and two *Oryx beisa*. The *Bubalus* skeleton and two of the three *Syncerus* were mounted so that not all characters were accessible. In addition to these specimens, some *Bos primigenius* limb bones from Ilford were seen, one *Syncerus* had previously been available in Nairobi for direct comparison with the bones of *Pelorovis*, and a mounted *Syncerus* skeleton was seen in Stockholm. The limb bones of the mounted skeleton of *Homoioceras nilssoni* were also seen in Stockholm ; characters 48, 51, 55, 62, 63, 69, 70, 77, 78, 82, 83 and 84 were not visible, and I have assumed that the animal resembles other Bovini in characters 48, 51, 63 and 78.

48. In *Hippotragus* (but to a lesser extent in *Oryx*) the great trochanter of the femur has a horizontal top edge and a tendency to antero-posterior lengthening,

which can be seen in lateral view. In Bovini the trochanter appears taller, and is without a tendency to antero-posterior lengthening ; it either has a slanted antero-dorsal edge descending to an anterior point or its whole front edge is evenly rounded. *Pelorovis* resembles Bovini (see Text-fig. 13).



FIGS. 12–15. 12, dorsal view of top of left femur 1952, BK II, 268 with anterior side towards top of the page ; 13, lateral view of great trochanter of same femur ; 14, lateral view of distal end of same femur ; 15, lateral view of great trochanter of a left femur of *Hippotragus*. *a* = high back of great trochanter, *a–b* = its slanted antero-dorsal edge, *c* = gluteus accessorius crest, *d* = vastus lateralis crest ; all these points are mentioned in character 48. *e–f* = wide lateral parts of articular head mentioned in character 50, *g* = front edge of lateral condyle mentioned in character 51.

In Hippotragini the ridge for the insertion of the gluteus accessorius is often at an angle to the lower part of the crest for the vastus lateralis which may continue horizontally behind it. In Bovini the gluteus crest often appears to continue the line of the vastus crest, and *Pelorovis* resembles them (Text-fig. 13). The condition in the Hippotragini is linked with the antero-posterior lengthening of the trochanter mentioned in the last paragraph.

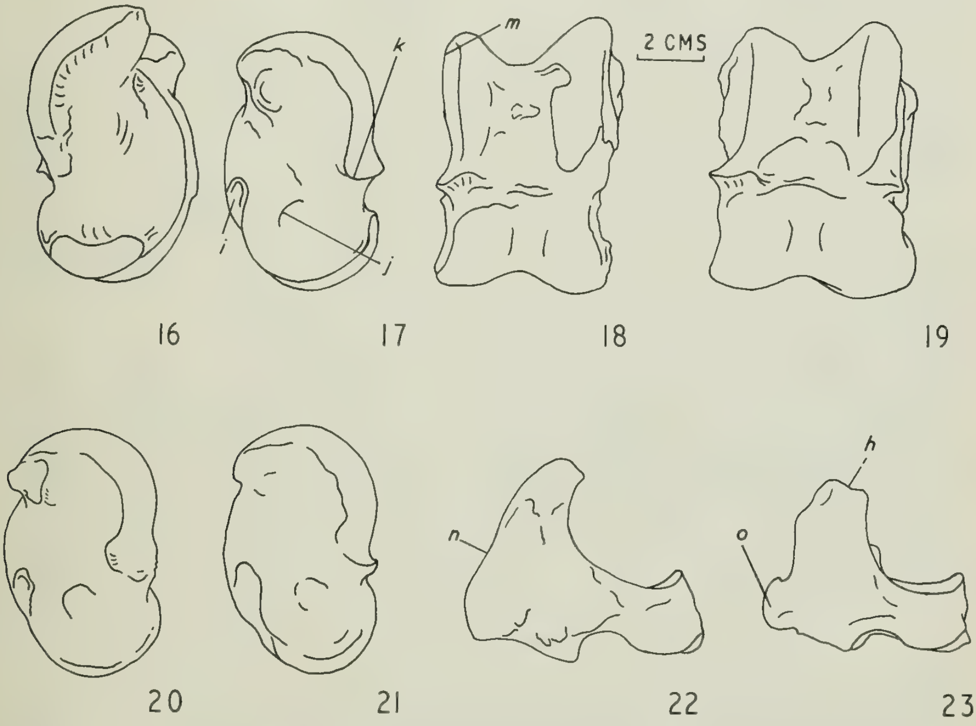
49. A deeper hollowing is present in anterior view between the articular head and the great trochanter in Hippotragini, *Syncerus*, the one *Bubalus* and probably *Homoioceras nilssoni* than in *Bos*. Linked with this character is the fact that *Bos* tends to have a steeper slope on the top edge of the articular head in anterior view

than the other genera, although this feature is not distinguishable in every bone. *Pelorovis* is unlike *Bos*, and like the other genera for this character (Pl. 4).

50. The articular head of the femur is less narrowed in its lateral parts in dorsal view in Hippotragini than in *Bos* and the single *Bubalus*. *Syncerus* and *Homoioceras nilssoni* have a condition intermediate between Hippotragini and the other Bovini, and *Pelorovis* agrees with *Syncerus* (Text-fig. 12).

51. The distal lateral condyle of the femur is more sharply pointed anteriorly in *Oryx* than in *Hippotragus*, Bovini or *Pelorovis* (Text-fig. 14).

52. The patellar fossa on the femur is wider in Hippotragini than in Bovini; within the Bovini some individuals of *Bos* may have it still narrower. It is wide in *Pelorovis* as in Hippotragini (Pl. 4).



Figs. 16–23. 16–18, lateral, medial and anterior views of left astragalus 1957, BK II, 1413; 19, anterior view of a fossil astragalus with different proportions from those of *P. oldowayensis* astragali; 20, medial view of astragalus of *Bos gaurus*; 21, medial view of astragalus of *Syncerus*. 22, medial view of a naviculo-cuboid of *P. oldowayensis*; 23, medial view of a naviculo-cuboid rather smaller than others belonging to *P. oldowayensis*. i = incision for naviculo-cuboid as mentioned in character 56, j = ridge for astragalo-metatarsal ligament mentioned in character 57, k = ridge for medial malleolus of tibia mentioned in character 58, m = position of projection mentioned in character 59. n = back edge of the naviculo-cuboid, o = localized projection at its base, h = top edge separate from back edge; all these points are mentioned in character 60.

53. A middle patellar groove is present at the top of the cnemial crest of the tibia in Hippotragini, but less markedly or not at all in Bovini or *Pelorovis* (Pl. 4).

54. The lateral articular facet at the top of the tibia has an upturned lateral edge in *Oryx* but not in the other genera being considered or in *Pelorovis* (Pl. 4).

55. The medial malleolus of the tibia is shorter in *Syncerus* than in the other genera or *Pelorovis* (Pl. 4).

56. There is a deep incision for the naviculo-cuboid at the back edge of the medial side of the astragalus in Bovini and *Pelorovis* but not in the Hippotragini (Text-fig. 17).

57. The ridge for the astragalo-metatarsal ligament on the medial side of the astragalus is weaker in *Syncerus* than in the other genera or *Pelorovis* (Text-fig. 17).

58. This ridge is level with the ridge for the base of the medial malleolus of the tibia in Hippotragini. In *Syncerus* and the *Bubalus* individual it may be lower, but in *Bos* the ridge for the malleolus is also low, and so the two ridges are at the same level. *Pelorovis* is most like Hippotragini, *Syncerus* and the *Bubalus* (Text-fig. 17). This character must be linked with 55 above, and one can say that the tibial-astragalus articulation of *Syncerus* differs from that of *Pelorovis* by having a shorter medial malleolus of the tibia, and *Bos* differs from *Pelorovis* by having a lower astragalar facet for the tibia's medial malleolus.

59. The back part of the top of the medial side of the astragalus projects slightly away from the main mass of the bone in *Oryx* in anterior view. This does not occur in any other genus or in *Pelorovis* (Text-fig. 18). The astragalus of *Homoioceras nilssoni* has a backwardly-directed extension in this position.

60. The naviculo-cuboid is a relatively deeper bone in Hippotragini than in Bovini or *Pelorovis*. This is most noticeable in lateral view.

61. The back edge of the medial side of the naviculo-cuboid is slightly or much curved in Hippotragini ; it tends to be straighter in Bovini and sometimes has a localized backwards projection at its lower end, and a top edge separate from its back edge. *Pelorovis* agrees with the Bovini (Text-figs. 22, 23).

62. Both front and back metapodials of *Syncerus* and the metacarpals of *Bos primigenius* are more antero-posteriorly compressed than in the other genera considered here or *Pelorovis*.

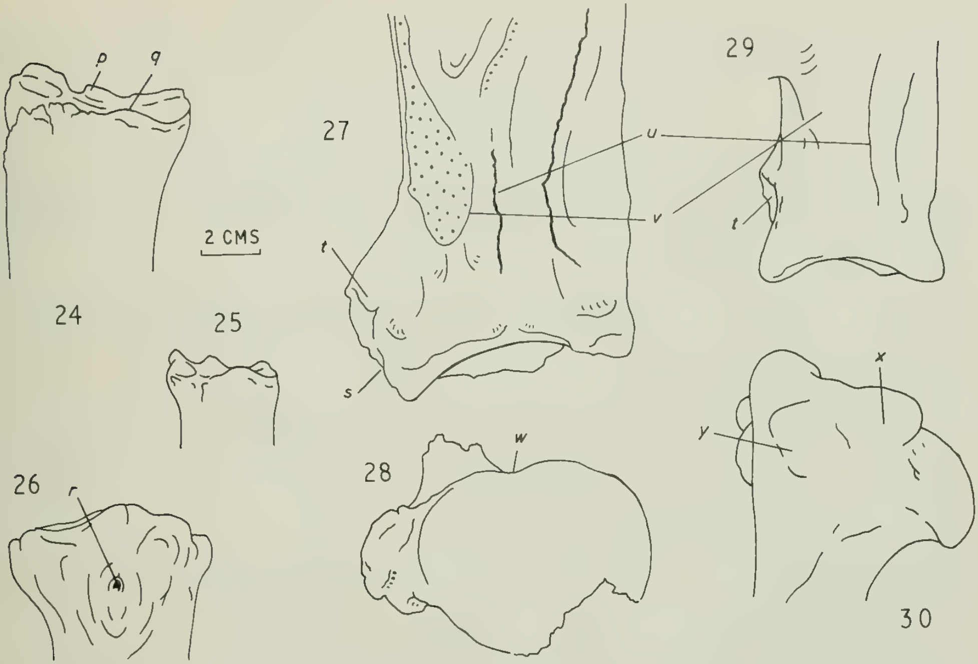
63. The back part of the naviculo-cuboid facet on the metatarsal rises high above the level of the immediately adjacent ectocuneiform facet in Hippotragini, and therefore has a strongly curved outline in medial view. This is not seen in Bovini or *Pelorovis* (Text-figs. 24, 25).

64. In medial view the ectocuneiform facet of Hippotragini is upcurved ; this is not seen in Bovini or *Pelorovis* (Text-figs. 24, 25).

65. In *Hippotragus* the foramen at the top of the posterior surface is situated on the medial side of the midline. This is less obvious in *Oryx* while in Bovini and *Pelorovis* the foramen is situated centrally (Text-fig. 26).

66. The distal anterior and posterior foramina of the metapodials are absent in *Syncerus*, or disappear earlier in adult life than in the other genera and *Pelorovis* (Pl. 5).

67. The tuber scapulae is low and strongly projecting in Hippotragini, i.e. its



FIGS. 24–30. 24, medial view of top of left metatarsal 1952, BK II, 275 ; 25, medial view of top of left metatarsal of *Hippotragus* ; 26, posterior view of top of left metatarsal 1952, BK II, 275 ; 27, lateral view of left scapula stem 1952, BK II, 183 ; 28, ventral view of glenoid facet of 1952, BK II, 183 ; 29, lateral view of left scapula stem of *Bos gaurus* ; 30, lateral view of proximal end of left humerus of *Hippotragus*. p = back of naviculo-cuboid facet mentioned in character 63, q = edge of ectocuneiform facet mentioned in character 64, r = foramen at top of posterior side of metatarsal mentioned in character 65. t = tuber scapulae, s = height of base of tuber scapulae above rim of glenoid facet mentioned in character 67, w = indent in lateral side of glenoid facet mentioned in character 68, v = base of spine of scapula, u = front of teres minor hollow mentioned in character 69. x = posterior eminence of lateral tuberosity of humerus mentioned in character 71, y = infraspinatus insertion mentioned in character 72.

ventral edge in lateral view rises from the rim of the glenoid facet and passes far in front of the facet. The tuber is higher in Bovini, but generally projects as far or almost as far as in the Hippotragini. In *Bos gaurus* it has an excavation on its antero-lateral side. *Pelorovis* most resembles Bovini other than *B. gaurus*. (Text-figs. 27, 29).

68. The lateral side of the glenoid facet on the scapula is indented in Bovini and *Pelorovis*, but not in Hippotragini (Text-fig. 28).

69. In Bovini there is a tendency for the teres minor cavity on the scapula not to pass so far forwards as the base of the spine ; this is less clear in *Syncerus* than in *Bos* and the single *Bubalus*, although it is not possible to tell *Syncerus* from every specimen of *Bos*. *Pelorovis* is like the Hippotragini or *Syncerus* (Text-figs. 27, 29).

70. The lateral tuberosity of the humerus is low in Hippotragini, i.e. it does not rise far above the bicipital groove in anterior view. It is higher in Bovini, except that two out of the five available *Syncerus* were intermediate between other Bovini and Hippotragini. In *Pelorovis* the tuberosity is low (Pl. 4).

71. *Syncerus* and *Homoioceras nilssoni* have a smaller posterior eminence behind the lateral tuberosity of the humerus than in *Bos* or the *Bubalus* individual. In the Hippotragini the eminence is perhaps still smaller but is antero-posteriorly lengthened and sometimes approaches having a posteriorly directed point. *Pelorovis* resembles *Syncerus* (Pl. 4; Text-fig. 30).

72. The front of the infraspinatus insertion is level with the front edge of the humerus in lateral view in *Bos*, the *Bubalus* individual and *Homoioceras nilssoni*, but lies slightly behind the front edge in *Syncerus* and Hippotragini. *Pelorovis* agrees with *Bos*, *Bubalus* and the *Homoioceras*. (Pl. 4; Text-fig. 30).

73. The bicipital groove at the top of the humerus is more frequently narrowed in anterior view in *Bos* than in the other genera or *Pelorovis* (Pl. 4).

74. The coronoid fossa at the distal end of the humerus is more shallow in Hippotragini than in Bovini or *Pelorovis* (Pl. 4).

75. The medial condyle at the distal end of the humerus is tall in *Hippotragus* and perhaps in *Homoioceras nilssoni*, but lower in other Bovini and *Oryx*. *Pelorovis* is like *Hippotragus* (Pl. 4).

76. The medial side of the medial articular facet at the top of the radius projects as a rim in anterior view in *Bos* and *Homoioceras nilssoni* but not in the other genera or *Pelorovis* (Pl. 4).

77. The postero-medial part of the medial facet has a greater area in *Bos* than in Hippotragini. Two out of four *Syncerus*, the one *Bubalus* and *Pelorovis* are like Hippotragini.

78. The lateral facet at the top of the radius is antero-posteriorly long in *Oryx* and some *Hippotragus*, but often short in the other genera being considered. *Pelorovis* (Text-fig. 34) agrees with Hippotragini, but is not convincingly different from Bovini.

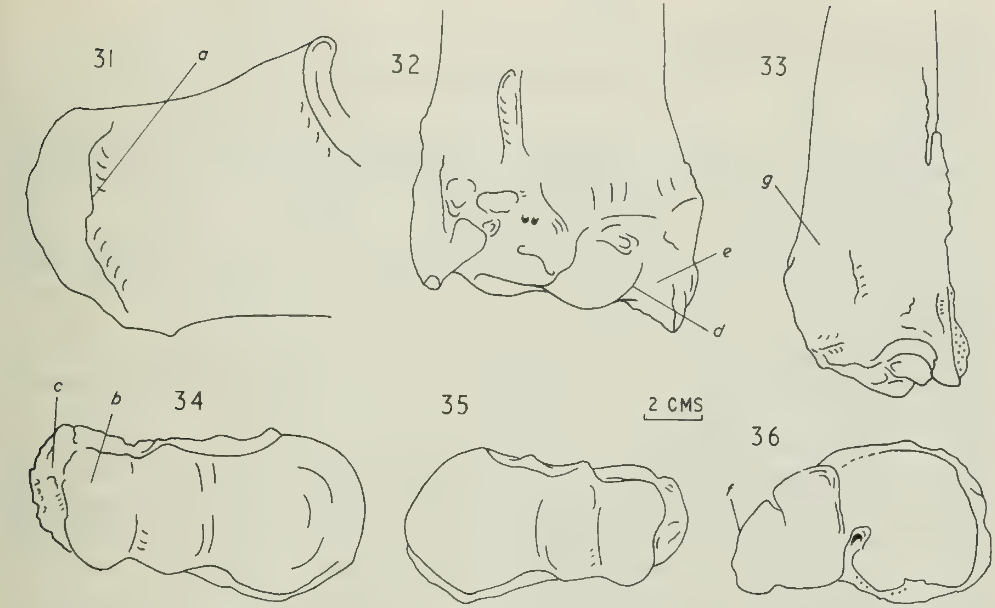
79. The lateral tubercle at the top of the radius is larger in *Oryx* than in *Hippotragus*, and intermediate in the Bovini and *Pelorovis* (Text-fig. 34).

80. The distal ends of radii of Bovini and *Hippotragus* appear swollen in lateral view, but this is not so for *Pelorovis* except in specimen 1955, BK II, 294 which is smaller than the other fossils and may therefore be a separate species (Pl. 4; Text-fig. 33).

81. The ridge between the posterior surfaces of the scaphoid and lunate facets at the distal end of the radius tends to be more slanted or less marked in *Syncerus*, the single *Bubalus* and *Homoioceras nilssoni* than in *Bos* or Hippotragini. *Pelorovis* is like the former group (Text-fig. 32).

82. The tubercle towards the front of the dorsal facet of the scaphoid is more sharply marked in *Bos* than in other genera or *Pelorovis*.

83. The bottom edge of the medial side of the scaphoid is less indented in *Syncerus* and *Hippotragus* than in other genera or *Pelorovis*. Correlated with this



FIGS. 31–36. 31, medial view of left olecranon 1952, BK II, 273 with its front edge towards top of page; 32, posterior view of distal end of same radius; 33, lateral view of distal end of left radius 1955, BK II, 294; 34, dorsal view of top articular surface of right radius 1953, BK II Extension, 425 with the anterior edge towards bottom of page; 35, dorsal view of left radius 1955, BK II, 294; 36, dorsal view of top articular surface of left metacarpal 1957, BK II, 1037 with anterior edge towards top of page. *a* = high origin of flexor carpi ulnaris muscle which is a peculiarity of *Pelorovis*, *b* = lateral facet mentioned in character 78, *c* = lateral tubercle mentioned in character 79, *e* = scaphoid facet and *d* = ridge between scaphoid and lunate facets mentioned in character 81, *g* = swollen distal end of radius mentioned in character 80, *f* = edge of unciform facet of metacarpal mentioned in character 85.

is the absence of a projection towards the posterior end of the upper surface of the magnum-trapezoid.

84. The projecting back edge of the lunate is narrowly pointed in *Hippotragus* in medial view, but not in the other genera or *Pelorovis.*

85. The unciform facet at the top of the metacarpal is angled in *Hippotragus* but not in *Pelorovis*, *Oryx* or Bovini (Text-fig. 36).

Among the limb bone characters of *Pelorovis* were three which might be valid as specific or generic characters, but which were not seen in Bovini or Hippotragini. These were the small sustentaculum on the calcaneum, the antero-posteriorly long infraspinatus insertion on the humerus (Pl. 4), and the flexor carpi ulnaris origin on the medial side of the olecranon which extended almost to the top of the bone (Text-fig. 31).

86. Bovini have wider cervical vertebrae than Hippotragini. This may be owing to allometry at least in part, but the long cervical vertebrae of a large form

like *Taurotragus* show that allometry need not be the only determining factor. *Pelorovis* agrees with Bovini.

87. Bovini and *Pelorovis* have deep ventral hollows on the atlas for the para-occipital processes.

88. The vertebrarterial foramina on the axis (Text-fig. 7) are smaller in *Bubalus, Syncerus, Homoioceras nilssoni* and Hippotragini than in some *Bos*. *Pelorovis* agrees with the former group.

89. The openings of the foramina transversa are nearer to the front and back edges of the side of the centrum on the third cervical in Bovini and *Pelorovis* than in Hippotragini. This difference is not visible on the more posterior cervical vertebrae.

90. The transverse processes are separate from their ventral flanges as far forwards as on the third cervical in Bovini and *Pelorovis*. In Hippotragini the separation occurs only in the more posterior cervical vertebrae.

91. The neural spines of the 4th, 5th and 6th cervical vertebrae are not so forwardly slanted in Bovini or *Pelorovis* as in Hippotragini.

The results of comparing length measurements of *Pelorovis* limb bones with those of two *Syncerus caffer* and three *Bos gaurus* are shown in Text-fig. 37. These Bovines were chosen for comparison because they were available and were of a similar massiveness to *Pelorovis*. One mounted *Bubalus* could only be measured for its femur (Text-fig. 9), humerus and radius, and has not been shown. It is seen that *Pelorovis* has a relatively long radius and short humerus, and also that the metapodials of *Syncerus* are noticeably short. Measurements of least thickness

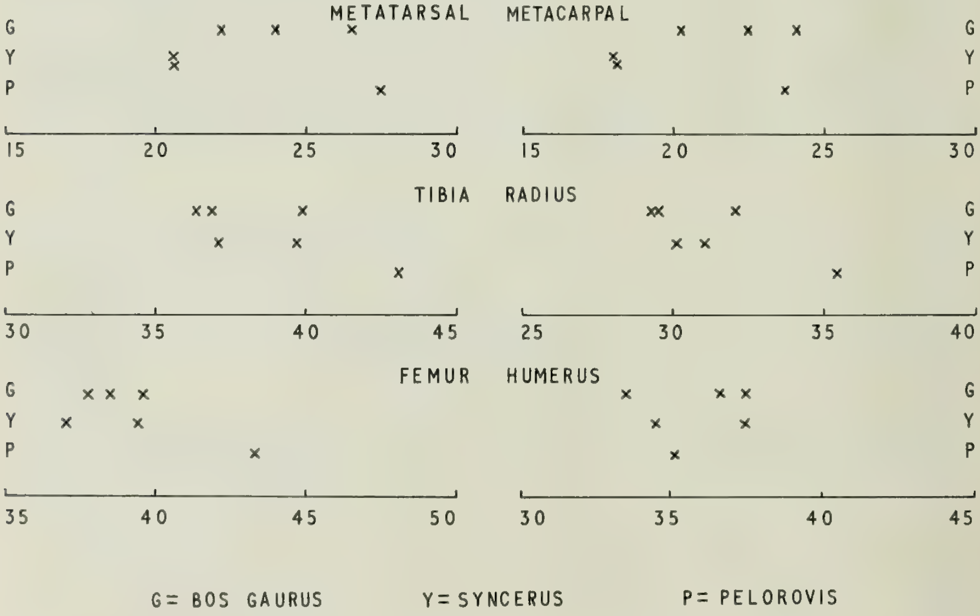


FIG. 37. Lengths of long limb bones. Measurements in cm.

of each limb bone in relation to its length failed to show reliable differences between these genera.

Colbert & Hooijer (1953 : 120) found fossil *Bubalus bubalis* to have shorter metapodials than *Bos gaurus*.

It is possible to assess numerically the differences of the other genera from *Pelorovis* in the 91 characters listed above. Character 2 was taken as the two characters face length and skull width ; character 16 was taken as the relative width of the nasals irrespective of skull length ; characters 63 and 64 were taken as one ; three characters were added to the total to represent the possibly valid limb bone characters of *Pelorovis* which were not seen in other forms ; characters 10, 22, 47 and 79 were omitted as not being sufficiently different among the forms compared ; and characters 11 and 20 were omitted as being not applicable to *Pelorovis*. This procedure left 43 skull characters and 45 limb bone and vertebrae characters for comparison, a combined total of 88. For *Bubalus* characters 62 and 82 were omitted, and this genus was assumed to be like other Bovini in characters 63, 78 and 85. Characters 82, 83 and 84 were omitted for *Bos primigenius*. Characters 16, 19, 25, 26, 28, 29, 36, 55, 62, 69, 70, 77, 82, 83 and 84 were omitted for *Homoioceras nilssoni*, it was assumed to resemble other Bovini in characters 48, 51, 63 and 78, and it was not checked for the three unique limb bone characters of *Pelorovis*.

In the following table is listed the number of differences which each form shows from *Pelorovis* ; the figures in brackets show the number of characters used in each comparison ; and the last column shows the number of differences which would be expected if 100 characters had been used in the comparisons, i.e. it is the readings of the third column converted to percentages of the corresponding figures in brackets.

	Skull characters	Limb bone and vertebrae characters	All characters	All characters out of 100
Syncerus . . .	19 (43)	13 (45)	32 (88)	36
Bubalus . . .	21 (43)	11 (43)	32 (86)	37
Bos gaurus . .	24 (43)	20 (45)	44 (88)	50
Bos primigenius .	18 (43)	19 (42)	37 (85)	44
Homoioceras nilssoni .	10 (36)	5 (34)	15 (70)	21
Oryx . . .	16 (43)	24 (45)	40 (88)	45
Hippotragus . .	26 (43)	25 (45)	51 (88)	58

The points to be noted from this table are :

1. That the Hippotragine *Oryx* appears as so little different from *Pelorovis* in its skull characters ; this is principally owing to the tooth similarities of the two genera.
2. That *Bubalus* appears as hardly more different from *Pelorovis* than *Syncerus* ; yet my opinion is that *Bubalus* is certainly much further phyletically from *Pelorovis* than is *Syncerus*.
3. That *Homoioceras* appears as the animal phenetically closest to *Pelorovis*, and as considerably closer than the living African buffalo. Even if the three unique characters of *Pelorovis* were added to the total for *Homoioceras* as differences, its final reading would still be only 25.

Conclusions

From the examination of skull characters it appears that the question of whether a fossil is assignable to the Hippotragini or Bovini may best be decided by reference to the following characters : the position and shape of the parieto-frontals suture, the level of the back of the nasals, whether the ethmoidal fissure is absent or present, the position of the infraorbital foramen, the level of the median indentation at the back of the palate, whether the basioccipital is triangular or more nearly quadrangular, and the size of the foramina ovales. The first of these characters is not applicable to *Pelorovis*, but it agrees with the Bovini in the remainder except for the level of the palatal indentation. In addition its large size and the posterior insertion of the horn cores tell for Bovine affinities. In most characters which *Pelorovis* shares with either of the Hippotragine genera—usually *Oryx*, there is also a resemblance to a Bovine genus ; the level of the palatal indent is the only firm resemblance to Hippotragini.

For the sake of completeness, three further points must be made. Firstly, the Lower Pliocene Hippotragini of Europe and China show a forwardly-indented parieto-frontals suture whenever this feature is visible, their ethmoidal fissure may be absent or very reduced, their foramina ovales are small, and *Sinotragus* has a well marked preorbital fossa.

Secondly, keels on the horn cores are present in many Bovini but not in Hippotragini apart from the early *Prosinotragus* and *Sinotragus* and possibly some others in which they may appear in connection with the transverse compression.

Thirdly, the earlier Bovine or Boselaphine genera *Selenoportax* Pilgrim, *Parabos*, *Proamphibos*, *Hemibos* and *Leptobos* all show (or all contain species showing) horn cores more divergent than in Hippotragini, and if the horn cores have any curvature in anterior or dorsal view it involves a reapproach of the tips or at least a lessening of the angle of divergence. Such a curvature is not seen in Hippotragini.

Within the Bovini, the *Hemibos-Bubalus* group has (or has retained) keels on its horn cores, and *Hemibos* already has the basicranial axis quite strongly angled on that of the face. The specialized vomer at the back of the palate may be connected with aquatic habits, and other distinctive characters such as the posterior expansion of the nasals and the lateral flanges at their anterior ends could also be connected with this.

Leptobos has preserved a basicranial axis nearly in line with the facial axis, but the closely related *Bos* has developed wide frontals and posteriorly inserted horns, and in so doing has presumably increased the bending of the basicranial axis on the face. Some *Bos* species have such posterior horn cores that they overhang the occipital surface at their bases. Keels are absent on the horn cores, or have been lost earlier than in *Hemibos* and *Bubalus*, on the other hand the ethmoidal fissure is not always absent in this stock. One learns from *Bos* that facial length is not a reliable character for use in classification above the species level, since there are striking differences of skull proportion between cattle and bison.

Homoioceras and *Syncerus* have neither wide frontals nor horn cores placed so far posteriorly as in some *Bos* species ; it seems possible that they too have evolved a bending of the basicranial on the facial axis, as in *Hemibos* and perhaps *Bubalus* and *Bos*. They have a tendency to flattening of the horn cores and consequently may possess irregular back and front keels. P_4 has a closed anterior part of its medial wall.

It is the absence of wide frontals, of keels on the horn cores, of a posterior contact of the vomer with the palate, and of an ethmoidal fissure, as well as the possession of an anterior medial wall of P_4, which allow *Pelorovis* to be considered as related to *Syncerus* despite the markedly posterior insertion of its horn cores. The closeness of the supraorbital pits and the extent of the premaxillary contact on the nasal are also like *Syncerus*, but are less convincing resemblances. *Pelorovis* is unlike *Syncerus* in the dimensions of its occipital surface, and in the width of the anterior tuberosities of its basioccipital. The latter character is likely to be directly related to the size of the horn cores, since *Homoioceras* and *Bubalus* both have tuberosities wider than in living *Syncerus* with its short horns.

The limb bones and vertebrae of *Pelorovis* are like Bovini rather than Hippotragini in the following characters : the shape of the great trochanter at the top of the femur ; no anteriorly directed point on the lateral condyle at the distal end of the femur ; no upturned lateral edge to the lateral facet at the top of the tibia ; no middle patellar groove on the tibia ; the deep incision at the back of the medial side of the astragalus ; no projection at the top of the medial wall of the astragalus ; naviculo-cuboid not deep ; no markedly curved outlines of the naviculo-cuboid and ectocuneiform facets at the top of the metatarsal ; the central position of the top posterior foramen of the metatarsal ; the shape and position of the tuber scapulae ; the indented lateral edge of the glenoid facet on the scapula ; the shape of the posterior eminence of the lateral tuberosity on the humerus ; the level of the front of the infraspinatus insertion ; the depth of the coronoid fossa on the humerus ; the size of the lateral tubercle on the radius ; the lack of a narrow projection at the back of the lunate ; the outline of the unciform facet at the top of the metacarpal ; the wide cervical vertebrae ; the deep ventral hollows on the atlas ; the position of the foramina transversa on the third cervical ; the separation of the transverse processes from their ventral flanges as far forwards as on the third cervical ; and the neural spines of the posterior cervicals not being very forwardly slanted.

In a number of other characters *Pelorovis* is like either or both genera of Hippotragini, but is also like or approached by *Syncerus* : the indentation between the articular head and great trochanter of the femur in anterior view, the wide lateral parts of the articular head in dorsal view, the teres minor cavity on the scapula reaching as far forwards as the base of the spine, the low lateral tuberosity of the humerus, the wide bicipital groove, the smallness of the posterior eminence of the lateral tuberosity, the absence of a rim on the medial side of the medial facet of the radius, the small area of the postero-medial part of the medial facet at the top of the radius, the more slanted or less marked ridge between scaphoid and lunate facets on the back of the radius, the poorly marked tubercle at the front of the dorsal facet of the scaphoid, the little indented bottom edge of the medial side of the scaphoid, and the small vertebrarterial foramina on the axis vertebra.

Pelorovis differs from *Syncerus* in not having the short medial malleolus of the tibia, not such a weak ridge for the astragalo-metatarsal ligament on the medial side of the astragalus, not such short or such antero-posteriorly compressed metapodials, and in having better marked foramina on the metapodials. The only resemblances of *Pelorovis* to Hippotragine limb bones but not to Bovini are the wide patellar fossa of the femur, the length of the lateral facet at the top of the radius, and the absence of a swollen distal end of the radius in lateral view.

From these results I believe that *Pelorovis* is a genus of Bovini, and since it shows slightly more phenetic similarity to *Syncerus* than to other Bovine genera it may well be phyletically related to this genus. The posteriorly inserted horn cores, long face, and the primitive occlusal pattern of the teeth make it very unlikely to have been the ancestor of *Syncerus*. It may be noted that so far as skull characters go, *Homoioceras* is more like *Pelorovis* than is *Syncerus* in its larger size, long horn cores with less emphasis on basal bosses, possibly having less compressed horn cores, the strengthened front part of the zygomatic bar beneath the orbit in *H. nilssoni*, a more anteriorly sited tooth row, and the wider anterior tuberosities of the basioccipital. Whether *Pelorovis* separated from the *Homoioceras-Syncerus* lineage before or after they became Bovini is not known. I take it to be Bovine rather than Boselaphine because of its large size, large posteriorly inserted horn cores, and the fairly hypsodont teeth, thus choosing to regard these characters as outweighing other more primitive tooth characters. If *Pelorovis* is accepted as a Bovine, then a qualification must be added to the use of the level of the median indentation at the back of the palate as one of the distinguishing characters between Hippotragini and Bovini.

IV A NOTE ON *BULARCHUS AROK* HOPWOOD

This species was described by Hopwood (1936 : 639–40) referring to material collected by the East African Archaeological Expeditions of 1931–32 and 1934–35. His generic diagnosis reads : " Bovidae of large size with massive horn cores, compressed from back to front, oval in cross section, closely approximated at their bases, curving crescent-wise upwards and downwards. So far as is known, the horns are in the same plane as the face and are not spirally twisted ". The specific diagnosis for *B. arok* is : " a *Bularchus* in which the span of the horn cores measures two metres, or more, from tip to tip ". Dr. G. E. Pilgrim is quoted as suggesting that *Bularchus* may be a very advanced member of the bubaline group in which the anterior keel on the horn cores has been suppressed. Two of the three specimens, M.14947–48, were supposed to have come from Bed IV at Olduvai and M.14949 from Bed II, but Mrs. M. D. Leakey has said (personal communication) that the matrix on the holotype, M.14947, shows that it is more likely to have come from the very top of Bed II, probably at the site now known as PLK (see also Leakey, 1965 : 106).

The holotype is a frontlet with horn cores ; it is poorly preserved compared with the finds of *Pelorovis* dating from 1952 and later years, but there can be little doubt that it is a specimen of Reck's *P. oldowayensis*. The compression of the horn cores is to be seen only at their bases where there has been some crushing, more distally the section becomes more nearly rounded as in other *Pelorovis*. There was possibly a longitudinal groove along the right horn core at least. So far as can be seen, the insertion of the horn cores overhung the occipital surface, and the angle of divergence of their bases was as in other *Pelorovis*. The ventral surface cannot be seen on the specimen as at present mounted.

The paratype, M.14948, is a frontlet with part of the left horn core. The core appears to be compressed, but part of its thickness may be missing. Taking the diameters of the horn core by the procedures described earlier gave readings of 10·0 × 15·2 cm., but an estimate for the complete horn core was *c.* 10·7 × 15·2 cm. In the former case the index of compression would be 65·8 and in the latter 70·4—a value easily possible for *P. oldowayensis*.

M.14949 is a horn core tip which is certainly not distinguishable from *P. oldowayensis*. Also in the British Museum (Natural History) is a pair of mandibular rami from Kanjera (M.15856) referred to *Bularchus arok* (see Kent 1942). The outbowings of the medial walls of the molars are not very localized and the ramus is quite deep under M_3. Both these characters are like *Pelorovis*, but P_4 is different from the Olduvai remains by having an open valley on the anterior part of its medial wall; I do not think that this difference is sufficient by itself to separate M.15856 from *P. oldowayensis*.

Measurements on the specimen were :

occlusal length M_1–M_3,	11·2 cm.
occlusal length M_2,	3.5 cm.
occlusal width M_2,	1·9 cm.
occlusal length P_2,	1·7 cm.

All teeth except P_3 are present on the right side but M_1 is damaged, on the left side P_3 to M_3 are present but M_3 is damaged. Also from Kanjera are a left upper molar, M.25676, measuring 3·35 cm. long by 2·35 cm. wide, incomplete upper molars, M.25677 and M.25688, an incomplete M_3, M.25692, a lower premolar, M.25678, and three tooth fragments, M.25679–81; all are inseparable from *Pelorovis*. There are also some unregistered fragments of Bovine cervical vertebrae with loose centrum ends. Unfortunately it is not possible to assign these remains, nor those of some Bovine limb bones from Kanjera, to *Pelorovis*, because there is definite evidence from an upper molar fragment, M.25715, of another Bovine at Kanjera with smaller and more advanced teeth.

In the National Museum of Tanzania, Dar es Salaam, is a large Bovid skull with long horn cores which was found with the herd of *Pelorovis* in 1952 (Pls. 5, 6). It shows some differences from the other skulls and had provisionally been taken to belong to *Bularchus* (Leakey 1965 : 45). Mandibular rami were found with the skull. It has been distorted complexly but not too severely. The back of the skull is twisted on the front part, and there has also been some transverse compression causing the orbits to be slightly too close. In addition the right orbital rim lies more anteriorly than its own internal parts and the base of the right horn core has obliterated the right temporal fossa. The left temporal fossa and horn core base are missing, perhaps because the contemporary men broke into the skull for the brain; on the other hand the skull was found in the clay of the gully and not on the land surface where the men have left their tools. The tooth rows are not in their natural positions and all the upper premolars are missing. Only the left anterior tuberosity is preserved on the basioccipital.

The skull is from a slightly younger individual than the complete skull of *Pelorovis oldowayensis*, providing that the less worn condition of the lower premolars and M_1 indicates age and not that the animal's food plants were less abrasive. It was probably four or five centimetres shorter than the complete *P. oldowayensis* skull, and there are no signs of sutures on the face bones. Measurements (in cm.) on this skull were :

Skull length	62·6
Skull width across the orbits	23·8
Distance from premaxilla tip to nearest point on the orbit	41·3
Length of horn core	160
Span of horn cores, tip to tip	216
Dorso-ventral diameter of horn core	9·3
Diameter at 90° to preceding diameter	15·3
Width between supraorbital foramina	13·3
Length from premaxilla tip to M^3	36·0
Length from M^3 to occipital condyle	26·7
Occipital height	9·6
Skull width across mastoids	28·2
Width across anterior tuberosities of basioccipital	*c.* 5·2
Width across posterior tuberosities of basioccipital.	8·1
Occlusal length M^1–M^3	10·4
Occlusal length M^2	3·6
Occlusal width M^2	2·8
Occlusal length M_1–M_3	11·75
Occlusal length M_2	3·5
Occlusal width M_2	1·9
Occlusal length P_2–P_4	6·9
Occlusal length P_2	1·8

The main points of difference between this skull and the other skull remains with which it was found are :

1. Its slightly smaller size. Despite its long horn cores, the skull appears to be slightly smaller than the complete skull of *Pelorovis* which I have taken to be from a female animal.

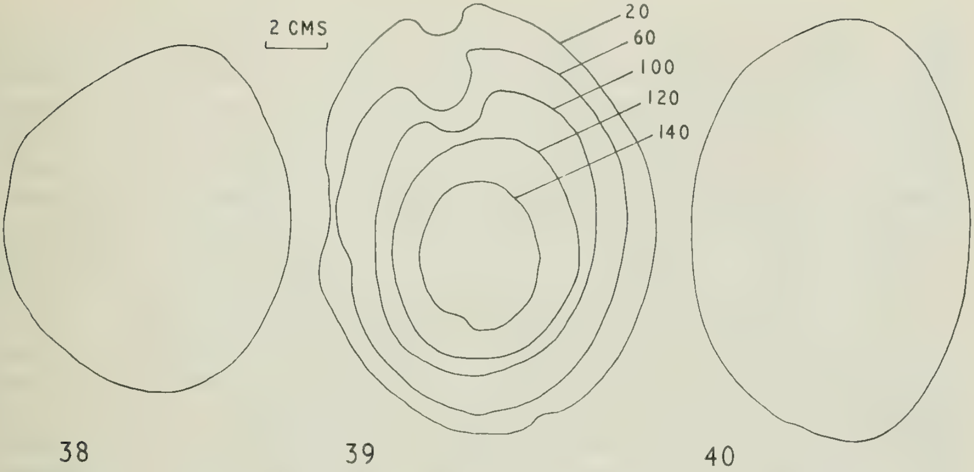
2. The horn cores are not so posteriorly inserted and do not overhang the occipital surface of the skull. There is no triangular depression at the top of the occipital surface.

3. The horn cores are more dorso-ventrally compressed than in *P. oldowayensis*, with an index of 60·8 compared with a range of 70·2 to 84·1 in the other skulls (Text-figs. 10, 40). They are also more nearly in a single plane than most of the horn cores of *P. oldowayensis*, i.e. there is a little less spiralization.

4. The width between the supraorbital pits expressed as a percentage of orbital width is 55·9 which compares with values of 42·3 and 53·2 for *Pelorovis oldowayensis*.

5. The zygomatic arch, continuing forwards under the orbits, is still deeper than in *P. oldowayensis* (Pl. 6), and more strongly concave on its ventral surface. This could be correlated with the mechanically less favourable position of the horn cores.

6. The tooth row is sited less anteriorly than in *P. oldowayensis*, as may be seen



FIGS. 38–40. Horn core sections at 20 cm. above base. 38, in the complete skull of *Pelorovis*; 39, in Pel 7; 40, in the second complete skull from BK II. Sections of Pel 7 are also shown at distances of 60, 100, 120 and 140 cm. above the base. If the horn cores pictured here are related to skulls with tooth rows in a horizontal position, then the ventral sides are on the right, the dorsal on the left and the anterior towards the foot of the page.

by comparing the positions of M^3 and orbit on Pl. 2, fig. 1 and Pl. 6, fig. 1 (the orbit being as far back in this skull as in *P. oldowayensis*). The ratio of the length from the premaxilla tip to M^3 as a percentage of that from the premaxilla tip to the nearest point on the orbit was *c.* 87·2 compared with 82·3 in *P. oldowayensis*.

7. The occipital surface of the skull has a reading of 34·0 for height as a percentage of width, which compares with readings of 40·7, 36·9 and 35·5 for *P. oldowayensis*.

8. The reading for the width between the anterior tuberosities of the basioccipital compared with the posterior ones was 64·2, which is different from the *P. oldowayensis* readings of 53·8, 57·6 and 58·4. This could be connected with the very great span of the horn cores as well as with their insertion in front of the level of the occipital surface.

9. The coronoid process of the lower jaw is slightly more sharply curved back than in *P. oldowayensis* (Pl. 6). This is correlated with character (6) above.

10. The horizontal ramus of the lower jaw is slightly more shallow beneath the molars.

11. P_4 on both sides has an open anterior part of its medial wall.

12. The anterior edge of each molar tooth in the lower jaw has a longer contact with the tooth in front than has *P. oldowayensis*.

The length of the lower premolar row as a percentage of the molar row is 58·7, which compares with values of 50·9 and 58·5 in *P. oldowayensis*.

In characters 2, 3, 6, 7, 9 and 10 this skull is more like that of *Syncerus* than is *P. oldowayensis*, but in 8 and 11 it is less similar. It is also nearer to *Homoioceras* in 2, 3, 6, 7 and 10.

One would not necessarily look for a greater amount of morphological difference between two Bovine species than exists between this skull and *P. oldowayensis*; on the other hand it is known for the Bovini to be very variable in their skull morphology (see Pilgrim 1939 : 263 on variability in *Hemibos triquetricornis* Rütimeyer), and this Olduvai skull is not at all beyond a possible range for *P. oldowayensis*. Because I cannot be certain, even with a whole skull, that this animal is specifically distinct from *P. oldowayensis*, I shall not name it. More Bovine remains diminishing the morphological gap between *Pelorovis* and buffaloes may well be found as further excavations add to faunal knowledge of the African Pleistocene.

V PHYLOGENETIC AND FUNCTIONAL CONSIDERATIONS

Some of the skull characters of *Pelorovis* may be distinguished as primitive, advanced or specialized. Primitive characters are those in which *Pelorovis* does not differ from Boselaphini or early Bovine genera such as *Pachyportax*, *Parabos* and *Proamphibos*; advanced ones are those in which it does differ from such early forms and which it shares with all or many of the later Bovine genera *Homoioceras*, *Syncerus*, *Hemibos*, *Bubalus*, *Leptobos* and *Bos*; specialized ones are those for which *Pelorovis* is distinctive although not invariably unique. This sort of assessment is not possible with all skull characters, nor with those of the limb bones and vertebrae.

Primitive characters, principally to be seen on the teeth, are: the poorly developed basal pillars, the absence of localized outbowings of the lateral walls of the upper molars, and the not very complex enamel walls of the central cavities.

The advanced characters of *Pelorovis* are: its large size and very large horns, the lack of an ethmoidal fissure, the lack of a preorbital fossa, and the fairly hypsodont teeth.

Its specialized characters are: the posterior insertion of the horn cores, anteriorly sited tooth row, and characters linked with these two.

One can suppose that with increasing size in any stock of Bovidae, the support of larger horn cores becomes a problem; this may be appreciated by comparing the post-orbital part of a horse's skull with the more massive construction of a larger Bovid. Within the Bovini, cattle have the horn cores set widely apart and far back. Thus the weight of the horn cores is supported above instead of in front of the occipital condyles, and the strain of support is widely spread across the back of the skull. In *Bubalus* and *Homoioceras* the horn cores are large, and set closer together in front of the level of the skull's occipital surface. Hence there is noticeable enlargement of the frontals for support, and, in *Homoioceras nilssoni*, strengthening of the zygomatic arch beneath the orbits as well. The curvature of the long horns is such that these skulls are most stable in an almost horizontal position. In *Pelorovis* the horn cores are set as far back as in cattle, although not so widely apart; their curvature carries the greater part of their weight so far behind the level of the occipital condyles that in life the animal must have counteracted by holding its head more nearly in the vertical position than do other Bovini. This is probably the reason for the strengthening of the zygomatic arch in an animal with its horn cores set so posteriorly. The complete skull from BK II at Olduvai, the identification of which is doubtful, has less posteriorly inserted horn cores than in *Pelorovis*, and their curvature takes them less behind the level of the occipital condyles. This might mean that in life the head was held a little less nearly vertically than in *P. oldowayensis*, except that in this skull the strengthening of the zygomatic arch is immense. Unless the skull of this animal was held nearly in the vertical plane, the curvature of its horn cores would have given less stability than there is in *Bubalus* and *Homoioceras* skulls.

The skull of *Pelorovis* shows a number of parallels with *Alcelaphus*, a genus which also holds its head in a more nearly vertical plane than other Bovidae. In both, the horn cores are inserted far back and close together, the face is long, there is sub-orbital strengthening of the zygomatic arch, an anteriorly placed tooth row, the median indent at the back of the palate passes well forwards, and there are small palatal fissures between premaxillae and maxillae. The 1952 find of *Pelorovis* was of a herd, and it might be thought that these animals could have been plains-dwelling grazers like *Alcelaphus*. However this may be carrying the comparison too far, and it is awkward to accommodate with the primitive occlusal pattern of the molars. The only ecological possibility likely for a Bovid which I would eliminate for *Pelorovis* would be eye-level browsing.

There are also a number of limb bone similarities between Alcelaphini and *Pelorovis* : the hollow between the great trochanter and articular head of the femur, the wide lateral part of the articular head, the wide patellar fossa on the femur ; the small posterior eminence and low lateral tuberosity of the humerus, the wide bicipital groove and the high medial condyle distally ; and possibly the non-swollen distal end of the radius in side view.

(It is none the less quite clear that *Pelorovis* is not an Alcelaphine because it has not such distinctive characters of one or more Alcelaphine genera as an abrupt alteration in the course of the horn cores, transverse ridges on the horn cores, excessively narrow nasals, a long contact of the premaxillae on the nasals, the premaxillae narrowing very little as they rise towards the nasals, the foramina towards the back of the palate being wide apart, the curved arcade of the tooth row, a strongly developed hypsodonty, the absence of basal pillars, or a complicated course of the enamel walls of the central cavities of the molar teeth.)

It is possible that while Africa is today inhabited by only one Bovine species which varies in morphology and ecology, it has been simultaneously inhabited at various times in the past by two or more species with more restricted ecologies.

The skull described in the last section of this paper is a possible example. There may also be mentioned two left upper molars, 1953, BK II Extension, 84 and 1957, BK II, 532 which are surely Bovine but which are smaller than the molars of *Pelorovis*, have more localized outbowings of their lateral walls, and central cavities which have perhaps too complicated enamel walls. The first one is 3·65 cm. long and 2·5 wide, the second 3·8 × 2·6. M.25715 in the British Museum (Natural History) is half a Bovine upper molar from Kanjera which is certainly not from *Pelorovis*, since it is smaller and definitely more advanced ; other specimens from Kanjera which could belong to the same species are M.25683, M.25697 and M.25705. In the Natron beds (see Isaac 1965), contemporary with the upper part of Bed II at Olduvai, is a Bovine left mandible fragment, WN 64,256, MP 1, which is perhaps a little smaller than *P. oldowayensis* and has more advanced teeth. It has retained M_2 and M_3, and they have large basal pillars, localized outbowings of the medial walls and noticeably narrowed lateral parts of the front and back lobes.

1957, SHK II, 671 is the tip of a horn core which appears to have been much shorter than *Pelorovis* horn cores and with less curvature. From its size it is likely to have belonged to a Bovine animal.

On the question of the ancestry of *Pelorovis*, *Simatherium kohllarseni* (Dietrich 1942 : 119–20, pl. 20, figs. 161, 163, 165) may be mentioned. It is the rear part of a damaged skull from the Bird River Region, Laetolil, found in deposits thought to be a little older than Bed I at Olduvai. So far as can be seen from the description and three photographs this animal has characters which fit it to be ancestral to *Pelorovis oldowayensis*. It is apparently about the size of a buffalo, and hence a little smaller than *P. oldowayensis* ; the horn cores arise behind the orbits but not so far back as in *P. oldowayensis*, and are larger than in its supposed contemporaries *Hemibos* and *Leptobos* in Eurasia although they look smaller than in *P. oldowayensis*. The horn cores are stated to have some degree of flattening, they either have no keel or have only a slight one in the position found in *Bos primigenius namadicus* and *B. acutifrons*, there is a wide shallow groove on the less damaged left horn core, and this horn core also shows a curvature comparable to that in *P. oldowayensis*. The frontals are raised between the horn bases ; in this the animal resembles *Hemibos* rather than *Leptobos*. Excavations have yet to reveal the ancestor of *Simatherium*.

The linking of *Pelorovis* with *Syncerus* does not illuminate the evolutionary origins of the Bovini. Previous work on Asian fossils has shown that the living *Bubalus* belongs to a group containing the extinct *Hemibos* and probably *Proamphibos* as well, and *Proamphibos* may be accepted as phyletically close to its Boselaphine contemporaries *Parabos* and *Pachyportax*. The *Bos-Leptobos* group represents another stock of Bovini in which the horn cores have more or less evenly rounded cross sections, and the central question is the history of keels on the horn cores. Have *Leptobos* and *Bos* lost keels so that their ancestors could be *Parabos*, *Pachyportax* or similar forms, or have they never had keels so that ancestors without keeled horn cores must be looked for?

Pilgrim (1939 : 141) supposed that the *Leptobos-Bos* ancestors did have keels, his evidence being that the early *Bos acutifrons* of the Pinjor stage had what could be the remains of a single keel, so too did *Bos primigenius namadicus* and at least one specimen of *Leptobos falconeri* (American Museum of Natural History, no. 19816, see Pilgrim 1937 : 817). It may also be noted that the Pleistocene bison of East Asia, discussed by Matsumoto (1918), appear from his diagrams to have had traces of keels. Both Merla (1949 : 147) and Rütimeyer (1878 : 117, 160, 167) were convinced of the Boselaphine relationship of *Leptobos*, and since all known genera of Boselaphini have keeled horn cores, there is a supposition that the ancestors of *Leptobos* also did.

The evolution of Bovine horn cores would thus be from the original more or less circular cross section of the earliest Bovidae such as the Miocene *Eotragus* Pilgrim, perhaps through some degree of lateral compression, then through a genus like *Protragocerus* Depéret of the European Upper Miocene (according to Thenius 1956 this genus should now include *Strepsiportax* Pilgrim from the Indian Chinji) which has at least the beginnings of keels, then an increase in size to *Pachyportax* and *Parabos* or their relatives. This would have been the latest stage at which the *Leptobos-Bos* group could have separated from the *Hemibos-Bubalus* group, since *Proamphibos* seems to be already approaching the vomer specializations of the latter group.

How can *Syncerus* and *Homoioceras* be fitted into such a scheme, assuming that they do have a Boselaphine ancestry? If my opinion of a relationship of *Pelorovis* to *Syncerus* is accepted, then *Pelorovis* reinforces the views of those who have held that Asiatic and African buffaloes are not very closely related, and provides no basis for connecting *Syncerus* with the *Leptobos-Bos* group instead. There is no diminution of the phenetic distance between the African Bovini and those of Eurasia. It is not clear how far Bovine evolution has consisted of a few long-independent lineages advancing gradually and often in parallel, or how far there have been repeated radiations of similar adaptive types at successive levels of overall advance.

There are many interesting chronological and ecological questions still to be answered on Bovine evolution in Africa alone : did *Pelorovis* overlap *Homoioceras* in time? There are very slender indications (e.g. the Natron Bovine mandible) that it could have done. Was there a difference in ecological requirements between the long faced *Pelorovis* and the short faced *Homoioceras* in any way comparable to that between the long faced *Bos primigenius* and the short faced bison? What are the ecological differences between cattle and bison anyway? How did *Bos primigenius* coexist with *Homoioceras antiquus* in North Africa? What was the other Bovine at Kanjera, of which we have half a molar tooth?

VI ACKNOWLEDGMENTS

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VII SUMMARY

Much Bovid material assignable to *Pelorovis oldowayensis* Reck has been excavated at Olduvai Gorge since 1952. This large species has horn cores inserted close together and so far behind the orbits that they overhang the occipital surface. The median indentation at the back of the palate comes well forwards, and the occlusal pattern of the teeth is not very advanced.

It is clear that *Pelorovis* is not a Caprine but is a member of the Bovini, and is phenetically nearest to the African genera *Syncerus* and *Homoioceras*. The reasons for this opinion are given in the conclusions to section III above. *Pelorovis* is very unlikely to have been an ancestor of *Syncerus* and *Homoioceras*, but published

photographs (Dietrich, 1942) give no indication that the Laetolil species *Simatherium kohllarseni* could not have been an ancestor of *Pelorovis*.

Material in the British Museum (Natural History) used to define *Bularchus arok* Hopwood (1936) is thought to be assignable to *Pelorovis oldowayensis*.

An almost complete Bovine skull excavated from site BK II at Olduvai in 1952 differs from *P. oldowayensis* in having horn cores less posteriorly inserted and its tooth row less anteriorly placed, rather more compressed horn cores, a wider occipital surface, wider anterior tuberosities of the basioccipital, and a shallower jaw ramus. It has a greater overall likeness to *Homoioceras* and *Syncerus*, and may be a separate species from *P. oldowayensis*.

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PLATE 1

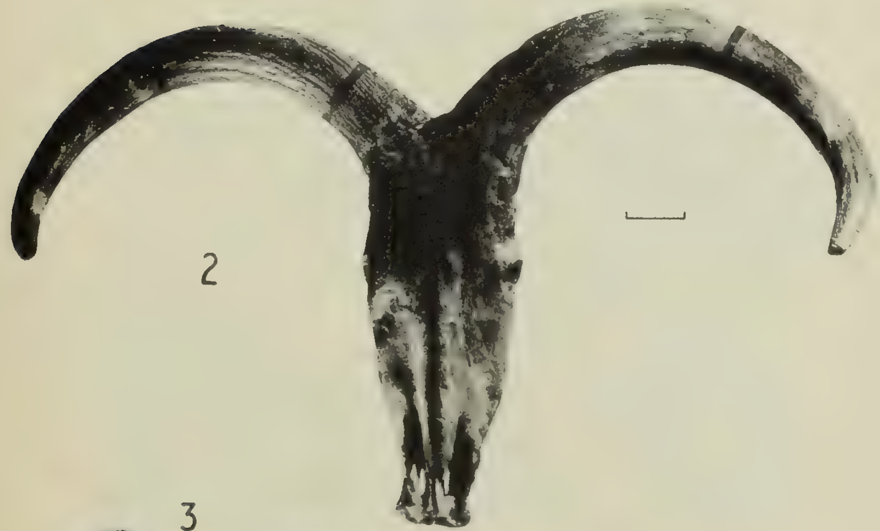
Pelorovis oldowayensis Reck

(Scales represent 10 cm.)

FIG. 1. The complete skull, Pel 1, during its excavation in 1952.
FIG. 2. Dorsal view of complete skull Pel 1.
FIG. 3. Palatal view of same skull.

1

2



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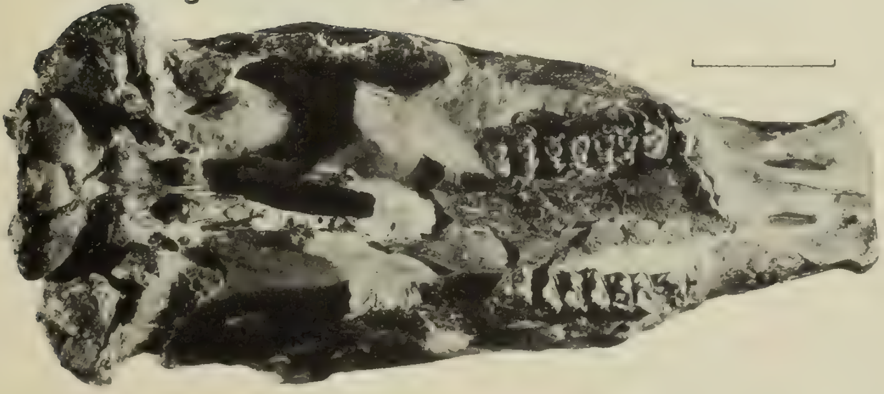


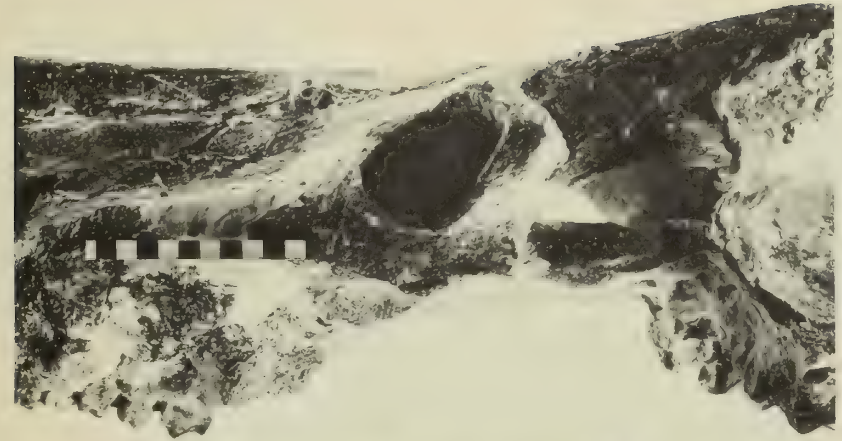
PLATE 2

Pelorovis oldowayensis Reck

FIG. 1. Lateral view of complete skull Pel 1. Scale marked in cm.

FIG. 2. Ventral view of back part of same skull. The arrow points to the indentation mentioned in character 35, and the scale represents 5 cm.

FIG. 3. The unnumbered frontlet. Scale represents 10 cm.



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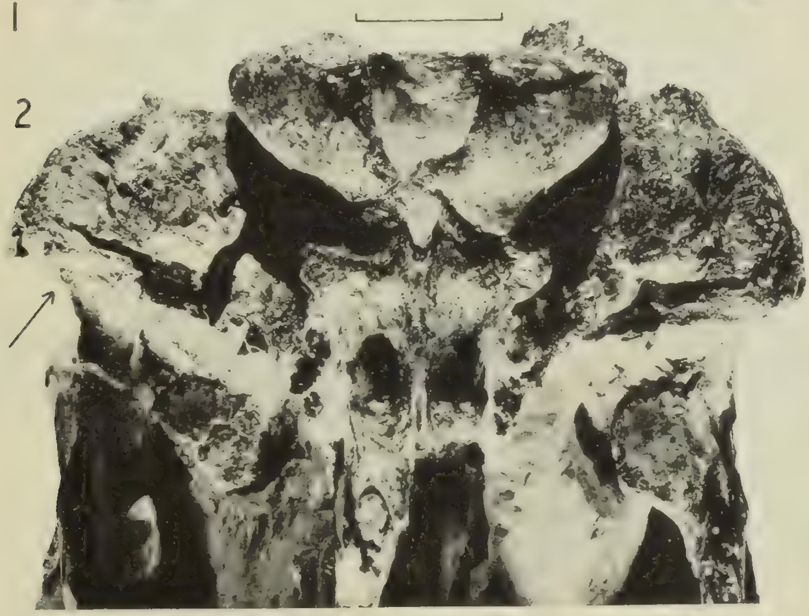

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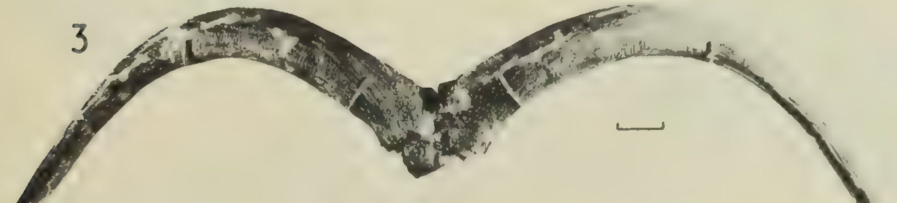

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PLATE 3

Pelorovis oldowayensis Reck

(Scales represent 5 cm.)

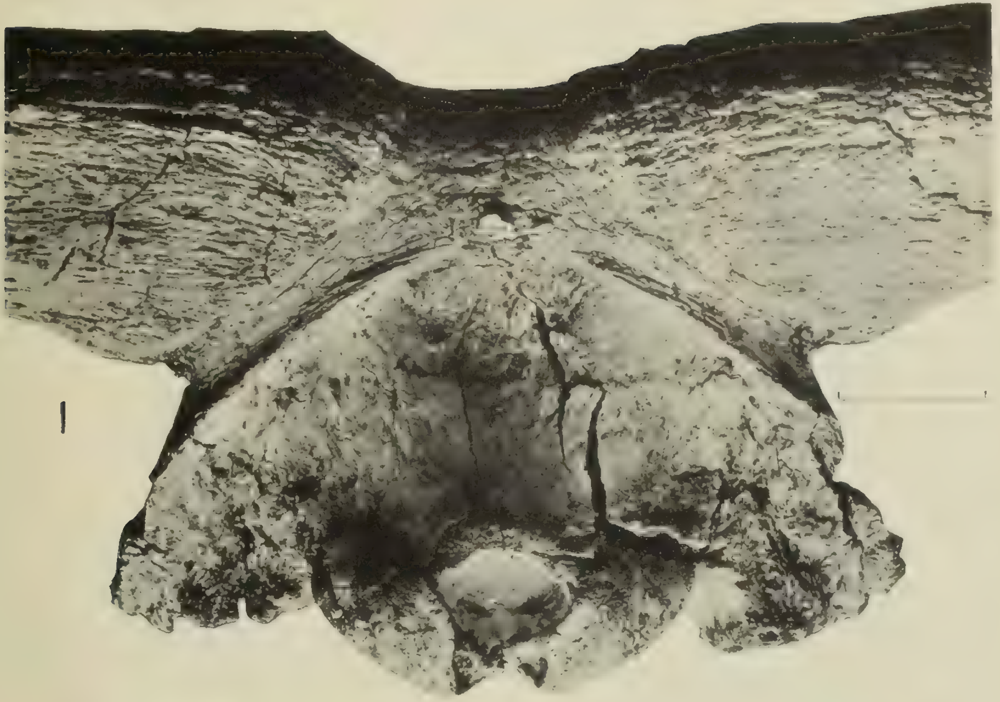
FIG. 1. Rear view of skull Pel 2 showing the complete occipital surface.

FIG. 2. Occlusal view of mandible 1952, BK II, 117.

FIG. 3. Lateral view of mandible 1952, BK II, 119.

FIG. 4. Occlusal view of upper teeth 1957, SHK II, 232.

FIG. 5. Lateral view of the bones at the front of the face in Pel 23. × = suture between premaxilla and maxilla.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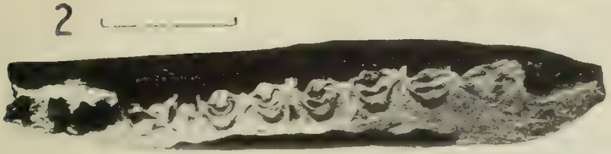
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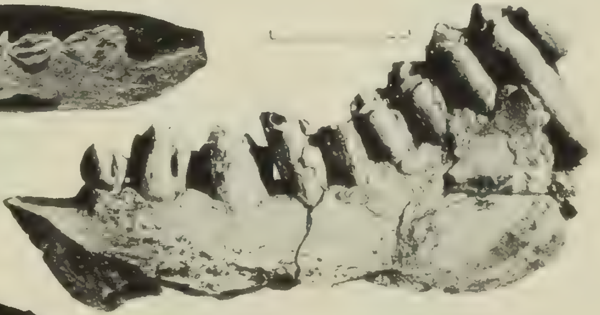
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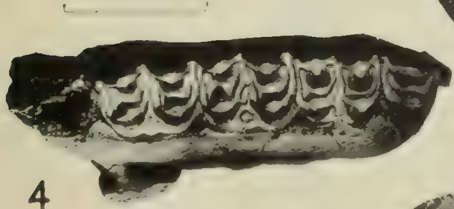
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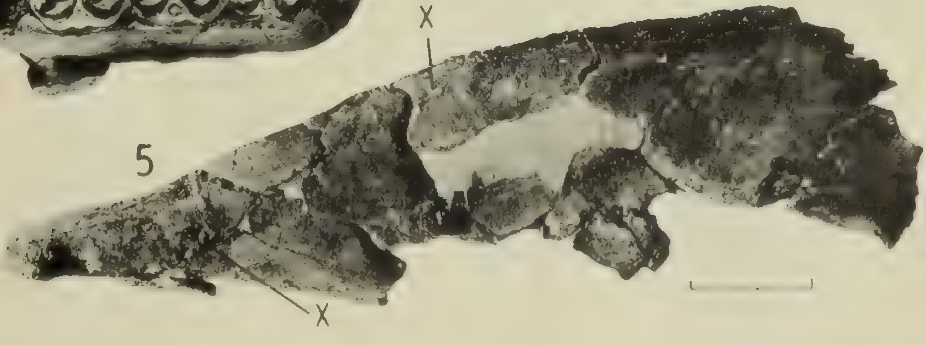
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PLATE 4

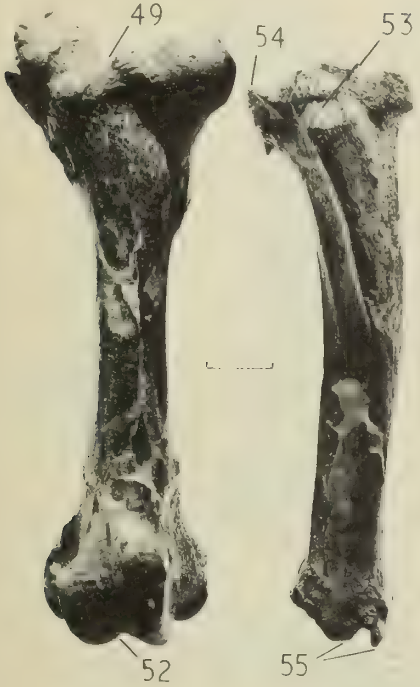
Pelorovis oldowayensis Reck

(Scales represent 5 cm.)

Top row from left : anterior view of right femur 1952, BK II, 267 ; anterior view of right tibia 1952, BK II, 269 ; anterior view of left humerus 1952, BK II, 271 ; anterior view of left humerus of ***Syncerus caffer*** (Sparrman) for comparison. The buffalo humerus has a tall lateral tuberosity (character 70).

Bottom row from left : anterior view of left radius 1952, BK II, 273 ; lateral view of same radius ; lateral view of left humerus 1952, BK II, 271 ; lateral view of left humerus of ***Syncerus caffer*** for comparison.

The numbers refer to the characters described in section III of the text.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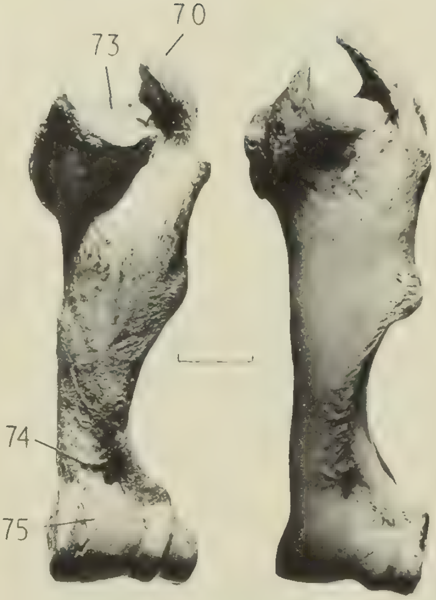
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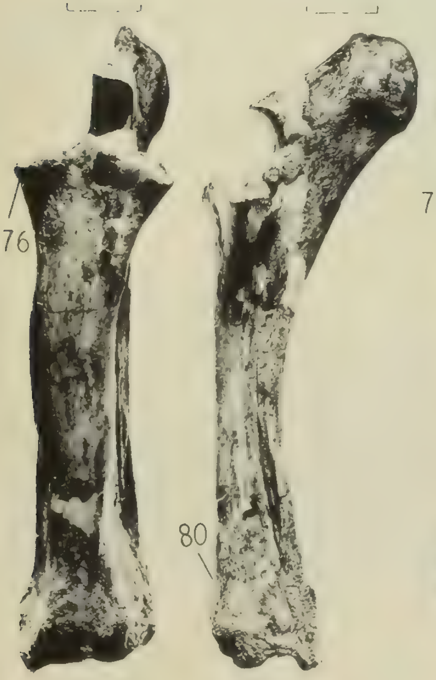
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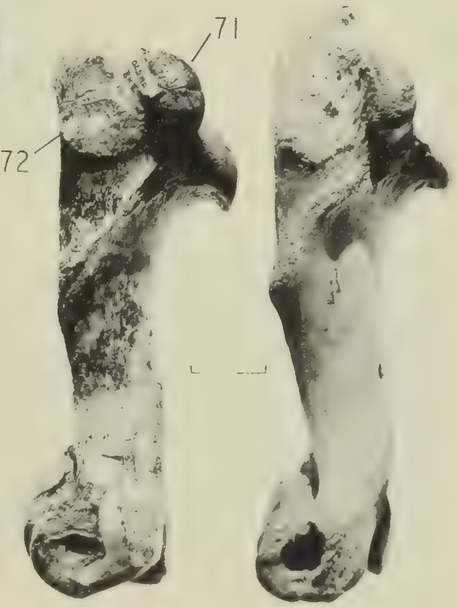

71
72

PLATE 5

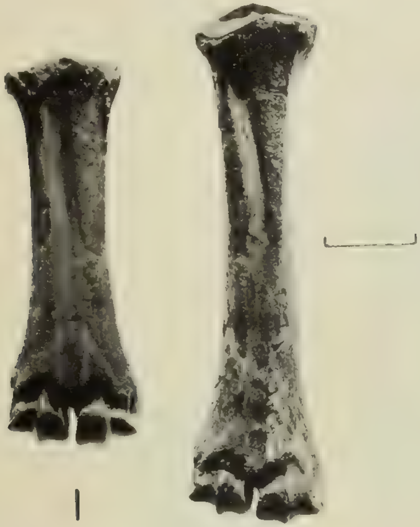
FIG. 1. Anterior view of metatarsals of ***Syncerus caffer*** (Sparrman) on the left and ***Pelorovis oldowayensis*** Reck on the right.

FIG. 2. Anterior view of metacarpals of ***Syncerus caffer*** on the left and ***Pelorovis oldowayensis*** on the right.

The scale for Figs. 1 and 2 represents 5 cm.

FIG. 3. Anterior view of second complete skull from BK II mentioned in section IV of text. This skull may not belong to ***Pelorovis oldowayensis***. Scale represents 10 cm.

FIG. 4. Palatal view of same skull. Scale represents 5 cm.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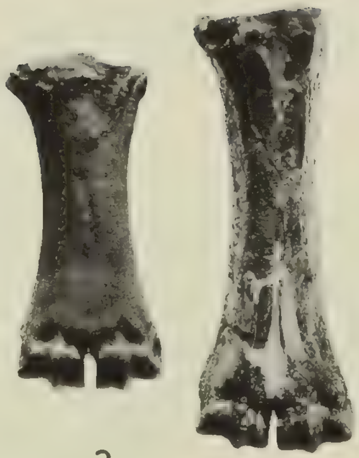
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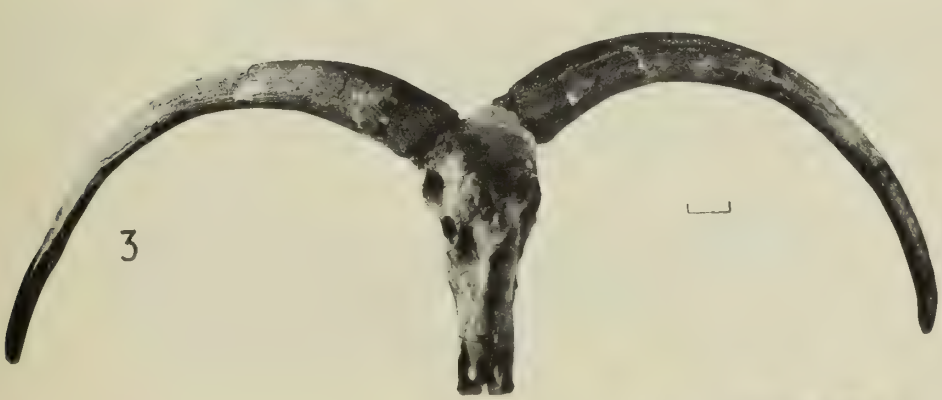
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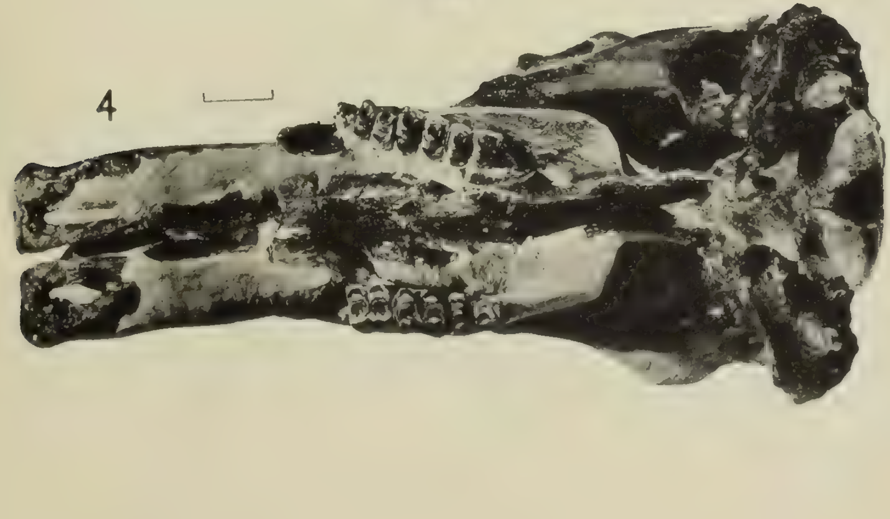
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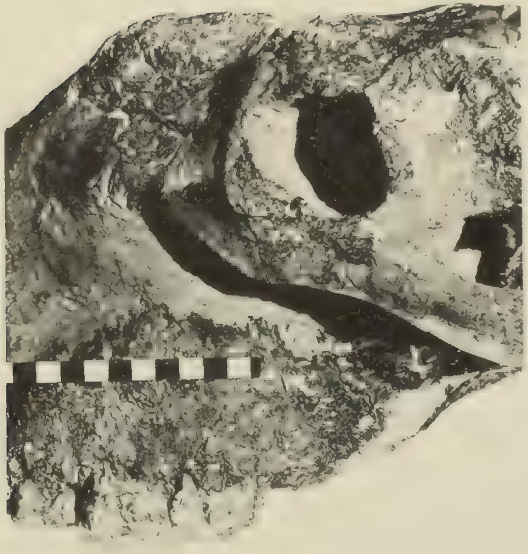
PLATE 6

FIG. 1. Lateral view of second complete skull from BK II to show the strength of the front of the zygomatic bar beneath the orbit. Scale in cm.

FIG. 2. Medial view of mandible from second complete skull from BK II (above) compared with lateral view of mandible of ***Pelorovis oldowayensis*** Reck from skull Pel 1 (below). Scale represents 5 cm.

FIG. 3. Occlusal views of lower teeth of second complete skull from BK II (above) compared with those of ***Pelorovis oldowayensis*** (below). Scale represents 5 cm.

1



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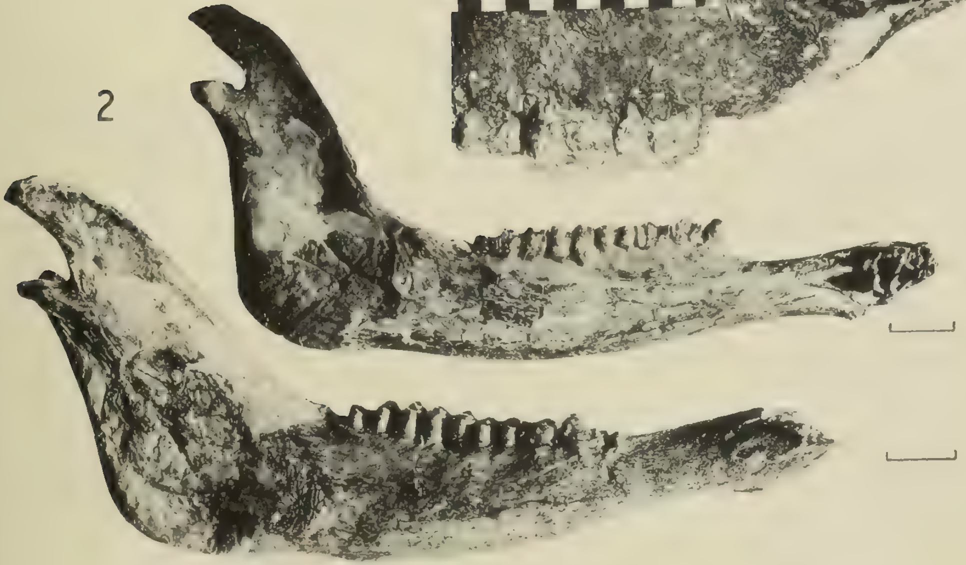

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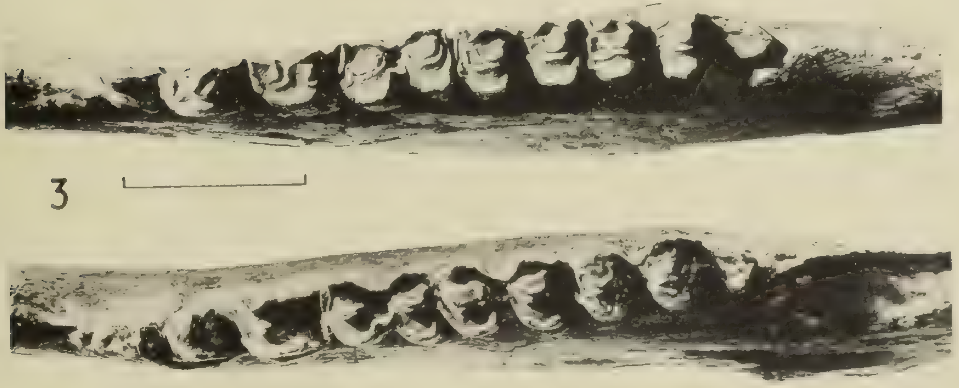

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NATURAL HISTORY

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